The Cutaneous Sensory Input to the Spino-cervical Tract of the Cat and the Cortico-fugal Modulation of Transmission from the Forelimb Component

Thesis

by

Jeremy Peter Heath

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SUMMARY

Section I - Literature Review

The literature is reviewed with special reference to knowledge of cutaneous afferent fibres and their representation in spinocervical tract fibres in the lumbar spinal cord of the cat. Attention is drawn to the paucity of information about forelimb afferents and their representation in the cervical spinal cord. The control of transmission through ascending sensory pathways and in particular the spinocervical tract is discussed. Finally relevant work on the somatosensory cortex and corticofugal inhibition is reviewed and comment is made on the influence of anaesthetics on our knowledge of sensory mechanisms.

Section II - Receptive fields and conduction velocities of identified spinocervical tract axons in the cervical spinal cord.

Recordings were made with micro-electrodes from single axons in the dorsolateral funiculus of the cervical spinal cord of decerebrate cats. Some of these axons could be designated on electrophysiological criteria as belonging to the spinocervical tract. Such axons conveyed tactile information qualitatively similar to that found by other workers in the lumbar cord. Quantitatively SCT axons with receptive fields in the forelimb were most common and were more frequently activated only by hair movement. Axonal conduction velocities were analysed in relation to the site and type of their afferent input.

Section III /

Section III - Homosegmental and heterosegmental inhibition of transmission through the spinocervical tract in decerebrate cats.

Discharges evoked in SCT axons by electrical and natural stimulation were tested for inhibition from other cutaneous nerves both by electrical and natural stimulation. Inhibition was most easily elicited from the homologous limb and least easily from the heterologous contralateral limb. Conditioning curves of segmental inhibition were plotted and were consistent with a pre-synaptic mechanism. In two spinalized decerebrate cats, only homosegmental inhibition was found.

Section IV - Ipsi- and contralateral corticofugal inhibition of transmission through the spinocervical tract.

Chloralose anaesthetised curarised cats were used to demonstrate corticofugal inhibition of spinocervical tract cells which were excited by electrical stimulation of the superficial radial nerve. Surface, sprung ball, stimulating electrodes were used to make a grid map of the cortical surface for areas of maximum inhibitory effect and glass micro-electrodes were used to stimulate the depth of the cortex. For both types of stimulation cathodal currents were most effective. Those areas of cortex eliciting most inhibition at a given current strength corresponded with the contralateral forelimb sensory receiving areas S.I and S.II. Weaker inhibition was elicited from the ipsilateral cortex. Conditioning curves of corticofugal inhibition were plotted.

Section V - Conclusion and general discussion of the function of the spinocervical tract.

The results of the previous sections are discussed in relation to present knowledge of the ascending sensory pathways and the problems they raise. Theories concerning the function of the spinocervical tract are discussed and it is postulated that the spinocervical tract may be concerned in the control of certain types of movement.

SECTION I

Literature Review

1. Cutaneous Receptors and the properties of their primary afferent nerve fibres

The introduction of the oscilloscope (Gasser and Erlanger 1922) and the development of single unit recording techniques (Adrian 1926) first with the capillary electrometer and later with Matthew's oscillograph heralded knowledge of specific cutaneous receptors. Adrian (1926, 1931) and his collaborators (Adrian and Zotterman 1926 a,b; Adrian and Umrath 1929; Adrian, Cattell and Hoagland 1931; Cattell and Hoagland 1931) showed that:

(1) The all-or-none law held for sensory nerve fibres.

(2) That the resultant discharge was a frequency code of the impinging stimulus.

(3) Harmful stimuli did not excite sensitive mechanoreceptors as efficiently as air jets.

(4) Mechanoreceptors (Pacinian corpuscles) were not excited by temperature.

(5) Activity in very small fibres was elicited by stimuli painful to man.

Controlled stimulation combined with unit recordings have enabled us to describe the properties of a number of distinct types of cutaneous afferent fibres and to correlate some of them with specific receptor structures (Iggo, 1974).

An examination of the electroneurogram of the frog's sciatic nerve (Erlanger and Gasser, 1930) showed three distinct populations of nerve fibre conduction velocities; on the basis of differential staining with osmic acid and

pyridine silver (Heinbecker, O'Leary and Bishop, 1933) it was thought that the slowest population was due to unmyelinated fibres. For technical and historical, rather than functional purposes, it is convenient to discuss the components of the electroneurogram separately. In frog sciatic nerve the 'B' wave encompasses sympathetic fibres whereas in mammalian peripheral nerves primary afferent fibres with analogous conduction velocities are present. These are denoted as 'A ' rather than 'B' (Erlanger and Gasser, 1937). The ranges of conduction velocity of the electroneurogram components are given in the following table.

Group of fibres	Conduction velocity ms^{-1}	Species
$A\alpha$	36-100 (Hunt & McIntyre, 1960c)	Cats
$A\delta$	9-35 " "	Cats
C	0.3-2.5 (Gasser, 1950)	Frogs

The range also corresponds to a minimum in the conduction velocity histogram of Burgess, Petit and Warren (1968). A group of fibres with conduction velocities between 9 and 2.5 ms^{-1} may also exist (Zotterman, 1939).

Primary afferent fibres and cutaneous receptors

Much work has been done on primary afferent fibres and the receptors they innervate. The information obtained has been extensively reviewed (Iggo, 1974; Burgess and Perl, 1973; Hensel, 1973).

Recording the response of single axons to careful stimulation of their receptive fields has shown that

information is transmitted as a frequency code and that mammalian receptors are more sensitive to a particular stimulus modality than to a particular sensory modality as defined introspectively. Mechanoreceptors have been found to have the widest range of conduction velocity; specific nociceptors are found in the Aδ range and unmyelinated fibres carry information from thermoceptors and mechanoreceptors of diverse sensitivities. Different types of mechanoreceptive fibres have been correlated with different histological structures (Iggo, 1977).

The above summary reflects the work of most electrophysiologists. However Wall and his collaborators (Wall, 1959 a, b; Wall and Cronly-Dillon, 1960; Wall, 1960; Wall and Dubner, 1972; Wall, 1973) have proposed that "A fibres are arranged in a monotonic continuum with threshold and diameter varying together" and that "the rate of adaptation is also strongly correlated with conduction velocity so that the lower the conduction velocity and the slower the adaptation the higher the threshold" (Wall, 1960).

This statement was made on the basis of a biased sample of 260 units, all but 4 of which had conduction velocities at or above 35 ms^{-1}. and were therefore in the Aα range. Thus Wall missed all the sensitive Down Hair afferents of Brown and Iggo (1967). More recently Wall has acknowledged the existence of sensitive C fibres (Wall and Cronly-Dillon, 1960) and of specific nociceptive receptors with axons conducting in the Aδ range (Wall, 1973).

Primary afferent fibres in the forelimb.

Most of the work on primary afferent fibres has been done on the hind limb of the cat (Brown and Iggo, 1967; Burgess, Petit and Warren, 1968). However some workers have studied afferent fibres from the forelimb either in the dorsal rootlets (Puletti, 1959; Pubols, Welker and Johnson, 1965), the dorsal columns (Uddenberg, 1968a), or in the peripheral nerves (Bromberg and Whitehorn, 1974). In the superficial radial nerve the slowly adapting type II receptors of Chambers, Andres, Duering and Iggo (1972) outnumber the slowly adapting type I units of Iggo and Muir (1969) by 2:1 whereas in the sural nerve slowly adapting type I (SAI) units are twice as numerous as slowly adapting type II (SAII) units. (Burgess, Petit and Warren, 1968; Bromberg and Whitehorn, 1974). Both studies used a similar sampling technique, micro-electrode recording, and as is the case in the hind limb both slowly adapting types had similar conduction velocity ranges so this difference is unlikely to be due to sampling bias even though this is present when Bromberg and Whitehorn's conduction velocity histogram is compared to Ekholm's (1967) fibre diameter histogram. However differences in conduction velocity spectra of hair types probably do exist as a comparison of Uddenberg's (1968a) hair conduction velocity histogram measured from the periphery with the summated hair histograms of Burgess, Petit and Warren (1968), both obtained with micro-electrode sampling reveals far fewer units with the conduction velocities expected of type D hairs in forelimb nerves.

Both Slowly and Rapidly adapting hair receptors are present in the carpal hairs of the forelimb of the cat. (Nilsson and Skoglund, 1965; Nilsson, 1976). Carpal hairs have a similar morphology, comprising a blood sinus and a complexity of nerve endings (Andres and Von During, 1973), and stimulus response, comprising an impulse train whose frequency depends on the degree of displacement, (Nilsson and Skoglund, 1965; Nilsson, 1976) to the vibrissae (Fitzgerald, 1940; Gottschalk, Iggo and Young, 1972).

Rosén and Sjolund (1973) have shown that the subdivision of group I (Lloyd, 1943) muscle afferents into Ia and Ib on the basis of electrical thresholds, which is valid for the hind limb semitendinosus muscle afferents (Coppin, Jack and McIntyre, 1969), is invalid for forelimb muscle afferent fibres; an assumption made by previous workers (Oscarsson, 1964).

Bromberg and Whitehorn (1974) noted all the receptor types of Burgess, Petit and Warren (1968) were present in the superficial radial nerve. Uddenberg (1968a) noted 13 claw units with slowly adapting responses to movement of the claw or a sensitive spot at the base of the claw. They were excited by cooling or hair movements and occupied a region of the fasciculus cuneatus distinct from that of touch units. Thus they are probably a separate group of receptors as proposed by Gordon and Jukes (1964) who noted them in the Gracile Nucleus.

Tables 1 and 2 summarise the properties of primary afferent fibres in the cat's hind limb and forelimb relevant to this thesis.

Table 1

This table shows the types of myelinated primary afferent fibres that have been categorised by single unit recordings in the peripheral nerves of the forelimb and hind limb or the fasciculus cuneatus and fasciculus gracilis of the cat.

+ indicates that their presence has been demonstrated.

- indicates that they have been shown not to be present.

? indicates that their projections have not been identified.

The nociceptive myelinated afferent fibres of Burgess and Perl (1967) described in the hind limb have not been included.

Comparison of Myelinated Primary Afferent Fibres in Forelimb and Hindlimb of the Cat

Receptor Type	Forelimb Nerve	Hindlimb Nerve	Fasciculus Cuneatus	Fasciculus Gracilis	References
"D" Hair	+	+	+	–	Bromberg and Whitehorn (1974) Brown (1968)
"G" or "G_2" Hair	+	+	+	+	Uddenberg (1968a) Brown (1968)
"T" or "G_1" Hair	+	+	+	+	Bromberg and Whitehorn (1974) Brown (1968)
Carpal Hair	+	–	?	–	Nilsson and Skoglund (1965)
Slowly Adapting "Type I"	+	+	+	–	Bromberg and Whitehorn (1974) Petit and Burgess (1968)
Slowly Adapting "Type II"	+	+	+	+	Bromberg and Whitehorn (1974) Brown (1968)
Rapidly Adapting Pad	?	+	?	+	Brown (1968)
Slowly Adapting Pad	+	+	+	+	Uddenberg (1968a) Brown (1968) Brown, Rose and Snow (1977b)
Field	+	+	+	+	Bromberg and Whitehorn (1974) Petit and Burgess (1968)
Slowly Adapting Claw	+	+	+	+	Uddenberg (1968a) Brown (1968) Brown, Rose and Snow (1976a)
Group 1 Muscle	+	+	+	–	Uddenberg (1968a) Landgren and Silfvenius (1969)
High Threshold Muscle	+	+	+	–	Uddenberg (1968a)
Low Threshold Joint	+	+	+	–	Körner and Landgren (1969) Burgess and Clark (1969)
Pacinian Corpuscle	+	+	+	+	Uddenberg (1968a) Brown (1968)

Table 2

This summarises some of the quantitative information gained from recordings from the axons of primary afferent fibres in the peripheral nerves and the dorsal columns. Note the differences in the prevalence and projections of primary afferent fibres with receptive fields in the hind limb and forelimb.

The following symbols denote the published work from which the data has been drawn:

oo Petit and Burgess (1968)

** Brown (1968b)

* Weighted means of Brown (1968b) and Petit and Burgess 1968

+ Uddenberg (1968a). All other forelimb data from Bromberg and Whitehorn (1974).

o Weighted means of Brown and Iggo (1967) (saphenous nerve) and Burgess Petit and Warren (1968) (sural nerve).

++ Burgess Petit and Warren (1968)

	Hindlimb				Forelimb		
Receptor Type	% Sample	% Projecting to the Dorsal Columns	Conduction Velocity ms^{-1}	% Slowing	% Sample	% Projecting to the Dorsal Columns	Conduction Velocity ms^{-1}
"D" Hair	16.6°	0.0**	19.7°	-	3.6	50.0	16.0
"G" or "G_2" Hair	21.0°	78.0°°	54.0°	50.2*	18.0	93.0	64.0
"T" or "G_1" Hair	15.0°	96.0°°	71.7°	57.6*	16.0	75.0	66.0
Slowly Adapting "Type 1"	20.4°	0.0°°	61.7°	-	9.0	75.0	58.0
Slowly Adapting "Type 11"	9.7°	100.0°°	53.9°	37.7*	14.0	80.0	59.0
Rapidly Adapting Pad	-	-	-	25.2**	-	-	-
Slowly Adapting Pad	-	-	-	-	1.0	-	-
Slowly Adapting Claw	-	-	-	-	4.4+	-	56.0+
Pacinian Corpuscle	4.1°°	100.0°°	65.0++	-	1.0+	-	-
Field	12.4°°	79.0°°	55.0++	56.0°°	19.6	100.0	64.0

2. The Flexor Reflex Afferents

The concept of flexor reflex afferents (F.R.A.) was first used systematically by Holmqvist and Lundberg (1961) although mentioned in previous papers (Eccles and Lundberg, 1959; Holmqvist, Lundberg and Oscarsson, 1960). Electrical stimulation of any part of the F.R.A. elicited a non-specific flexor reflex accompanied by the excitation of several spinal pathways ascending to higher centres. This term therefore comprises GpII and GpIII muscle afferent fibres, of Lloyd (1943), high threshold joint afferents and all but the lowest threshold cutaneous afferents. All these types of receptors were considered to produce central actions in "a pattern of functional unity". P.B.C. Matthews (1972) has criticised this umbrella concept as a "straight-jacket restricting thought and hence the precision of experiment". This is arguable not only for the GpII muscle spindle afferents but also for the cutaneous afferents. Carpenter, Engberg, Funkenstein and Lundberg (1963) noted that hind leg cutaneous afferents elicited different wave forms of dorsal root potentials in spinal and decerebrate cats. In spinal cats a short latency wave is present preceding a second wave which may only be obtained with higher stimulation strengths. In decerebrate cats this second wave is not present and as flexor actions are largely depressed in the decerebrate (Sherrington and Sowton, 1915; Eccles and Lunberg, 1959) this second wave only was considered to be due to the F.R.A. Thus the presence of a cutaneous component in the F.R.A. is

dependent on the animal preparation. In the intact animal the effect of the cutaneous component of the F.R.A. is also dependent on the animal's age. Windle (1929) noted that newborn kittens were "very irritable to tactile stimuli" whereas after 26 days the kittens were "less irritable and required greater stimuli to produce the same reaction". Skoglund (1960) found that in decerebrate newborn kittens pinching of one hind limb resulted in a withdrawal of that limb and complex movements of the contralateral hind limb resulting in a flexor reflex. Ekholm (1967) examined cutaneous reflexes in kittens in detail and found that spinalisation did not change the reflex pattern until an age of two to three weeks. Distal muscles were more sensitive to cutaneous reflexes. Thus as the kitten matures, either a change in the ratio of excitatory to inhibitory cutaneous inputs, or the increase in the gamma innervation of muscle spindles, or both, leads to a decline in the influence of cutaneous afferents on motorneurons.

The concept of the F.R.A. has been applied to ascending paths by Lundberg and co-workers (Lundberg and Oscarsson, 1960, 1961). Lundberg divided the tracts ascending the dorsal part of the lateral funiculus but not reaching the cerebellum, into one excited by non F.R.A. cutaneous afferent fibres and two others excited at short and long latency by the F.R.A. Hongo, Jankowska and Lundberg (1968) have shown that the spinocervical tract receives excitation from GpIII muscle afferents and thus the division of

pathways on the basis of the F.R.A. concept does not agree with electro-anatomical classifications.

In conclusion, the concept of the F.R.A. has simplified our understanding of the interactions of primary afferent axons, interneurones and motorneurones at the segmental level (Lundberg, 1964). Care should be taken when denoting afferent receptors to the F.R.A. particularly when electrical thresholds rather than mechanoreceptive properties are used to identify such afferent fibres. In particular the synapses on the flexor reflex circuits should not be thought of as the only or most important synaptic contacts of such afferent fibres.

3. The entry of Primary Afferent Fibres into the Spinal Cord.

Most afferent fibres enter the spinal cord by way of the dorsal roots. However as early as 1839 Magendie was not too sure of the absolute distinction of the dorsal roots (Liddell, 1960) and the concept of "Recurrent sensitivity" has been verified both anatomically and physiologically by Sherrington (1894), Dimsdale and Kemp (1966) and Kato and Tanji (1971) for myelinated fibres and by Coggeshall, Coulter and Willis (1973) and Clifton, Coggeshall, Vance and Willis (1976) for unmyelinated fibres. These latter workers showed that as many as 29% of the fibres in the third sacral ventral root were afferent; 67% of these had visceral and 23% cutaneous receptive fields.

The silver staining methods of Ranson (1913) and Szentágothai (1964a) show that in the dorsal rootlets 'C' fibres lie peripherally.

4. The Composition of the Grey Matter of the Spinal Cord.

Anatomists have used "synaptological" (Ramón y Cajal, 1952) and cytoarchitectonic (Rexed, 1952, 1954) methods to demarcate areas of the grey matter of the spinal cord. The latter method offers the possibility to both anatomists and physiologists of correlating structure and function with relatively easily definable areas of the grey matter. On the appearance of 100 μM thick, toluidine blue stained sections Rexed (1952) proposed nine laminae in each half of the spinal grey matter, six of which were in the dorsal horn. These laminae were particularly evident in kittens (Rexed, 1952) but could also be seen in 100μM thick unstained sections of adult spinal cord (Rexed, 1954). The lumbar and cervical enlargements showed particularly well developed Laminae III, IV and V. The latter intumescence being situated in segments C5 to C8 inclusive.

At the very tip of the dorsal horn is the tract of Lissauer containing C fibre afferent fibres (Ranson, 1914, a, b; Earle, 1952; Szentágothai, 1964a) which enter the Substantia Gelatinosa (Pearson, 1952). The lateral part forms a short propriospinal system connecting laminae II and III of adjacent segments. Wall (1962) has implicated the tract of Lissauer in the spread of Dorsal Root Potentials. In monkeys Kirk and Denny Brown (1970) have found that cutting the tract corrects the dermatomal expansion which is seen when neighbouring roots are sectioned distal to their ganglia. Christensen and Perl

(1970) found Lamina I cells responding, sometimes monosynaptically, solely to $A\delta$ nociceptors; nociceptive C fibres also excited some cells.

Rexed (1952) states that Lamina II corresponds with the substantia gelatinosa Rolandi and so does Ralston (1968b). However in the intumescences there is no discrete boundary between Lamina II and III and Sprague and Ha (1964) and Szentágothai (1964a) on synaptological grounds and Wall (1962) on physiological grounds include both laminae in "substantia gelatinosa Rolandi". Ramón y Cajal (1952) observed it to be lobulated in transverse section and Scheibel and Scheibel (1968) saw these lobuli as large, slightly radially oriented flat planes extending longitudinally in the cord.

Réthelyi and Szentágothai (1969) have seen pyramid shaped cells in the border of Laminae III and IV projecting into lamina II with both electron microscopy and Golgi techniques. They suggested that the glomeruli of these cells are the anatomical substrate for presynaptic inhibition of primary afferents which were seen to degenerate postsynaptically.

Rexed (1952) describes lamina IV as having large, 35 -45μM diameter cells intermingled with smaller cells and Réthelyi and Szentágothai (1973) and Scheibel and Scheibel (1968) postulated these are the cells of origin of the spinocervical tract. This has been confirmed by iontophoresis of procion yellow and horseradish peroxidase into electrophysiologically identified cells (Brown, House,

Rose and Snow, 1975; Brown, Rose and Snow, 1977a). These workers found large dorsal dendrites which rarely penetrated into lamina II. They also found axon collaterals giving off terminal branches in lamina IV, V and VI and have proposed that these cells may have a function at a segmental level.

Lamina V has a more reticulated appearance and corresponds to the "neck of the dorsal horn" of previous workers.

The terminations of primary afferent fibres in the grey matter has been much studied. C fibres have been traced to the medial part of Lissauer's tract (Ranson, 1914 a,b; Pearson, 1952; Szentágothai, 1964a) and are most numerous in laminae II and III (Ralston, 1968b). However little is known of their central terminations.

After cutting dorsal roots terminal degeneration can be found in the adjacent segments at nearly all depths of the grey matter; a particularly high concentration is seen in laminae III, IV, V and VI. (Sprague and Ha, 1964; Ralston, 1965; Scheibel and Scheibel, 1968, 1969). Degeneration in lamina II is not seen with the Marchi technique and many workers (Escolar, 1948; Ralston, 1965; Sterling and Kuypers, 1967) failed with the Nauta technique. However Szentágothai and Kiss (1949) succeeded. Using the less 'suppressive' Fink-Heimer modification of Nauta's technique Heimer and Wall (1968) showed that two days after cutting the roots massive degeneration was found in laminae I, II and III. It is likely that the degeneration

time is critical as Ralston (1968b) reports rapid removal of fine degenerating terminals.

Ramón y Cajal (1952) and Szentágothai (1964a) saw collaterals of primary afferent terminals in lamina IV rising to laminae II and III in silver stained preparations.

Recently Brown, Rose and Snow (1977b, 1978a) have recorded intra-axonally from primary afferent fibres in the lumbro-sacral cord and iontophoresed horseradish peroxidase into their axons and terminal arborisations. It was found that different types of mechanoreceptor axon gave off collaterals with characteristic terminal arborisations. Two thirds of their sample of Tylotrich and Guard hair activated mechanoreceptor axons ascended rostrally upon entering the spinal cord and only gave off collaterals to areas of the dorsal horn rostral to their point of entry.

Imai and Kusama (1969) have used Nauta techniques to uncover the longitudinal distribution of a single dorsal root's afferents in the cervical cord. They found ascending fibres tended to distribute to medial laminae IV and V and descending fibres to the lateral parts of these laminae in agreement with Sterling and Kuypers' (1967) results in the lumbo-sacral cord. The rostro-caudal extent of degeneration was considerable; over six ascending segments and seven descending segments contained degenerating fibres.

Wall and Werman (1976) have used antidromic

microstimulation in the grey matter of the lumbo-sacral cord to trace the extent of collaterals. They found that rootlets in the first lumbar segment projected as far caudally as the first sacral segment. The rostral dorsal root projections are likely to contain afferents to spino-cerebellar tract neurones both in Clark's column, which only extends as far caudally as L4 in the lumbar cord, and the rostral spino-cerebellar tract, whose cells are possibly found in upper cervical segments (Matsushita and Ikeda, 1975).

On electrophysiological grounds Wall (1962, 1964) has proposed that laminae II and III are the site of presynaptic inhibitory mechanisms. Futhermore Ralston (1968a) has seen degenerating post-synaptic elements of axo-axonic synapses in electron micrographs of these laminae after cutting the dorsal roots. Gray (1962) proposed that axo-axonic synapses are the substrate of presynaptic inhibition. However Eccles, Schmidt and Willis (1963 a,b) favour neurones encountered at depths of more than 2mm from the cord dorsum and on anatomical grounds Réthelyi and Szentágothai (1969) have suggested that the presynaptic elements of the axo-axonic synapses are large pyramidal cells in lamina IV.

5. The composition of the white matter of the spinal cord.

Tracts ascending in the white matter of the spinal cord and evoking short latency responses in the somatosensory cortex are classically regarded as conveying somaesthetic information whereas tracts eliciting responses in the cerebellum are regarded as conveying information used in the control of movement. However it has been known for a long time that many spinocerebellar axons convey purely cutaneous information (Yamamoto and Migajima, 1959; Lundberg and Oscarsson, 1960) particularly from the forelimb, and that for at least one type of receptor, the SAI, the dorsal spinocerebellar tract (D.S.C.T.) is the only known pure route to higher centres from the hind limbs (Mann, 1971). However information from slowly adapting I units may reach the cerebral cortex with relatively little modification of the stimulus-response relationship (Mountcastle, Talbot and Kornhuber, 1966). Hence the classical view that all somaesthetic information is conveyed by tracts eliciting short latency potentials in the cortex should be viewed with caution.

Functionally the spinocerebellar projection has been divided into at least twelve components (Oscarsson, 1973) and electro-anatomically into at least four components. The dorsal spino-cerebellar tract originates from cells of Clark's column (Lundberg and Oscarsson, 1960) and courses in the ipsilateral dorsolateral funiculus conveying

information from ipsilateral cutaneous and muscle receptive fields. Its forelimb equivalent, the cuneo-cerebellar tract, arises from cells in or near the external cuneate nucleus.

The ventral spino-cerebellar tract and its forelimb equivalent the rostral spinocerebellar tract contain more convergent tactile and exteroceptive information. The former crosses the midline to ascend in the contra-lateral ventral funiculus whilst the latter ascends ipsilaterally.

Of particular relevance to this thesis are

(1) The presence of D.S.C.T. somata in laminae IV and V below the caudal limit of Clark's column (Busch, 1961; Aoyama, Hongo, Kudo, 1973; Tapper, Mann, Brown, Cogdell, 1975) which according to Rexed (1954) is L3-L4. These could be responsible for confusions in the literature concerning the projections of spinocervical tract cells to the cerebellum.

(2) The location of forelimb spinocerebellar tract cells in Rexed's (1954) central cervical nucleus (Matsushita and Ikeda, 1975). These could be mistaken for forelimb S.C.T. cells.

The ventral spinal cord contains spinothalamic tracts. In the cat these do not elicit, at short latency, potentials in the cerebral cortex (Andersson, 1962) but their existence has been shown electrophysiologically in the cervical cord by Dilly, Wall and Webster (1968) and in the lumbar cord by Trevino, Maunz, Bryan and Willis

(1972). The former workers found their units in laminae V to VI whilst the latter found them deeper in laminae VII to VIII. Both groups of workers only found somatic action potentials with low amplitudes suggesting small cell bodies and because of this Trevino et al. used signal averaging to clarify their records, a procedure criticised by Able-Fessard, Levante and Lamour (1974) who denied the existence of a spinothalamic tract in the cat.

Anatomical evidence for a direct spinothalamic tract in the cat was until recently very weak as lesions which affect the lateral cervical nucleus would be expected to show degeneration in the thalamus (Landgren, Nordwall and Wengstrom, 1965). Morin and Thomas (1955) using the Marchi technique and Van Beusekom (1955) using Haggqvist methods failed to show a direct spinothalamic tract. Two possible reasons for this are; (1) that the spinothalamic tract is polysynaptic in the cat. Van Beusekom (1955) favours this explanation, and (2) the Marchi and particularly the Haggqvist methods do not stain fibres below 2μM diameter very efficiently (Haggqvist, 1936; Busch, 1961), and thus small fibres particularly if diffusely distributed would be missed. This latter explanation is also probable as Boivie (1971) using Fink-Heimer and Nauta techniques has demonstrated degeneration in the thalamus after lesions which do not involve the cervical-thalamic tract (cf Anderson and Berry, 1959; Mehler, 1969). This degeneration was found ipsilaterally in the magnocellular part of the geniculate body, the ventrolateral part of the posterior

nuclear complex, the zona incerta, the nucleus centralis caudalis, the nucleus parafascicularis and the nucleus centralis lateralis. However degeneration was not found in the nucleus posterolateralis in contrast to the previous workers who had also sectioned the cervico-thalamic system. Boivie did not observe a somatotopic organisation of the terminations.

In man and some primates the anatomical evidence for the existence of direct spino-thalamic tracts is clearer (Edinger, 1889; Mott, 1895; Collier and Buzzard, 1903; Bowsher, 1957). The electrophysiological characteristics of such units are also better defined (Willis, Trevino, Coulter and Maunz, 1974; Able-Fessard, Levante and Lamour, 1974).

A ventral and lateral tract are thought to exist. The cells of origin are large cells in the dorsal horn whose axons cross the anterior commissure and ascend in the contralateral ventral funiculus. In man (Bowsher, 1957) degeneration is found in the nucleus ventralis postero-lateralis. Electrophysiological studies have shown that in primates spinothalamic axons are excited by hair movement, weak and strong mechanical cutaneous stimulation, and joint and muscle inputs; intense thermal stimulation excited many of these cells. The cells of origin were in laminae IV to VI for units excited by weak stimuli and lamina I for cells only excited by intense stimuli. 100 out of the 186 units of Willis, Trevino, Coulter and Maunz (1974) responded to light stimulation of the skin. These

findings are compatible with the behavioural studies which suggest that the spinothalamic system subserves touch, itch, pain and temperature sensations (Walker, 1940).

The dorsal columns of the spinal cord contain ascending and short descending axon collaterals of dorsal root fibres (Ramón y Cajal, 1952). Only 25% of myelinated fibres entering the spinal cord at lumbar levels reach the dorsal column nuclei (Glees and Soler, 1951). Degeneration studies in primates show that particularly at lower thoracic levels caudal roots tend to lie medially in the fasciculus gracilis (Ferraro and Barrera, 1935; Walker and Weaver, 1942; Carpenter, Stein and Shriver, 1968).

In the cat post synaptic units have been identified electrophysiologically in both the fasciculus cuneatus (Uddenberg, 1968a, 1968b) and in the fasciculus gracilis (Angaut Petit, 1975). Rustioni and Dekker (1974) have shown the cell bodies and the terminations (Rustioni, 1973, 1974) of these units in the nucleus gracilis and nucleus cuneatus with the horseradish peroxidase and Fink-Heimer techniques. They terminate in the same part of the dorsal column nuclei as the cortico-fugal fibres, i.e. the multipolar cells with long sparsely ramified, radiating dendrites of Kuypers and Tuerk (1964).

In rodents the dorsal columns also contain cortico-spinal axons (King, 1910; Douglas and Barr, 1950).

Electrophysiological studies of the arrangement of dorsal root fibres within the dorsal columns (Werner and

Whittel, 1967; Whittel, Petrucelli, Sapiro and Ha, 1970) have shown that in the squirrel monkey the dermatomal organisation of the rootlets continues in the fasciculus gracilis at lumbar levels; the more caudal units coursing dorsomedially and the more rostral units ventrolaterally. Between lumbar and cervical levels the non-cutaneous receptors leave the dorsal columns and the cutaneous receptors are arranged as a series of bands with a discrete topographic organisation resembling that of the more rostral post synaptic elements of the dorsal column-medial-lemniscal system. In the cat electrophysiological investigators have favoured a functional organisation of the dorsal columns with hair follicle receptors coursing superficially with S.A. type II beneath these and joint receptors deeper still (Yamamoto, Sugihara and Kuru, 1956; Brown, 1968a; Uddenberg, 1968a). However the former authors observed receptors from the bladder and thoracic wall, and high threshold mechanoreceptors not observed by other workers. Glees and Soler (1951) observed that not all receptors which entered the dorsal columns reached the nuclei. By recording from lumbar dorsal roots (Lloyd and McIntyre, 1950; Petit and Burgess, 1968) or the lumbar fasciculus gracilis (Brown, 1968b) and antidromically firing units from high cervical levels it is possible to show which unit types project to the dorsal column nuclei. Lloyd and McIntyre (1950) showed that Gp.I muscle afferents from the hind limb do not reach the gracile nucleus and Brown (1968b) and Petit and Burgess (1968) showed that

guard and tylotrich but not down hair receptors, S.A. II but not S.A. I units, rapidly adapting pad receptors (probably including Pacinian corpuscles), slowly adapting pad and S.A. receptors at the base of the claws projected. Brown noted a few high threshold mechanoreceptors and S.A. I units but his sampling method was more vulnerable to post synaptic units which do in fact resemble these receptor types (Angaut-Petit, 1975).

Burgess and Clark (1969) showed that most hind limb joint receptors do not project to the dorsal columns.

Thus most axons with conduction velocities above the A.δ range in cutaneous nerves project up the dorsal columns. However differential slowing of conduction velocities occurs in the dorsal columns with the result that a receptor's mean conduction velocity may well fall in the A.δ range. This is illustrated in Table 2. It is seen that R.A. pad receptors are least affected by this slowing.

The forelimb projection to the cuneate nucleus shows marked differences with the gracile projection. Group I muscle afferents do project to the main and external cuneate nucleus (Oscarsson and Rosén, 1963; Landgren, Silfvenius and Wolsk, 1967; Rosén, 1969). So do S.A. type I receptors, claw receptors and high threshold muscle receptors (Uddenberg, 1968a; Bromberg and Whitehorn, 1974). Cortical potentials evoked by low threshold joint receptors from the fore but not the hind limb, are abolished by dorsal column section (Korner and Landgren, 1969). These

results are summarised in Table I.

Angaut-Petit (1975) found that 14.5% of her sample of fibres in the fasciculus gracilis with cutaneous receptive fields were post synaptic. Uddenberg's (1968b) data was biased towards these units and so no estimate can be made of their numbers in the fasciculus cuneatus. Receptive field characteristics suggest convergence of cutaneous primary afferents. Hair, light touch, temperature, joint movement, muscle afferents and deep pressure were effective stimuli. Some units had central latencies compatible with monosynaptic activation. Of particular interest was the observation that S.A. type I touch receptors might excite these units.

6. The spino-cervical tract.

Although anatomists have long recognised that there are cell bodies in significant numbers in the first two cervical segments of many species (Edinger, 1889; Cajal, 1952; Rexed and Strom, 1952; Rexed, 1954), the spino-cervical tract has not been recognised as a distinct tract until relatively recently.

In 1955 Morin showed that cortical potentials were evoked in S.I and S. II at shortest latency when the dorso-lateral funiculus was intact. He also demonstrated that the lateral cervical nucleus (L.C.N.) was the site of retrograde chromatolysis after the medial lemniscus had been sectioned. However Morin felt that the axons eliciting the cortical potentials were "in all probability in the dorsal spino-cerebellar tract".

Although Morin is usually given the credit for discovering the spinocervical tract, Shuster in 1906 found that a tract in the dorsolateral funiculus must be ablated to alter the orienting reaction of dogs to light tactile stimuli. As both Morin and Shuster were investigating a physiological phenomenon and as neither realised that the tract concerned was a separate anatomical entity from the D.S.C.T. or the dorsal columns respectively, Shuster's claim has at least chronological priority. Hereafter axons ascending to the lateral cervical nucleus in the most medial and superficail part of the dorsolateral funiculus will be referred to as the spino-cervical tract. (Van Beusokom, 1955; Lundberg and Oscarsson, 1961).

The question of whether the spino-cervical tract is a completely separate entity from the D.S.C.T. is disputed by both anatomists and physiologists. Ramón y Cajal (1952) saw spherical cells with curved hairy dendrites in his "noyau du faisceau cerebelleux". As this name suggests Cajal's Golgi stained material led him to believe that the L.C.N. was a relay nucleus of the D.S.C.T. for he saw inputs from collaterals of these axons. Rexed and Brodal (1951) found retrograde degeneration in the L.C.N. after lesions of the cerebellum but Brodal and Rexed (1953) found preterminal degeneration in the nucleus after lesions of the ipsilateral dorsolateral funiculus as low as the spinal segment S.3, which is below the level of the cells of origin of the dorsal spino-cerebellar tract; they also showed that primary afferents do not reach the L.C.N. Rexed and Strom (1952) maintained that the L.C.N. was only activated from the forelimb possibly being the forelimb homologue of Clarke's column. Ha and Liu (1961, 1962, 1963, 1966; and Morin, Kitai, Portnov and Demirjian, 1963) also state that there is a spino-cerebellar projection to the L.C.N. More recent workers have not favoured this idea. Grant, Bovie and Brodal (1968) re-examined Rexed and Brodal's (1951) material and using the successive degeneration method of Sherrington and Laslett (1903) to eliminate the dorsal spino-cerebellar tract, found no degeneration in the cerebellum with the Nauta technique after ablating the lateral cervical nucleus. Horrobin (1966) failed to excite antidromically cells in the L.C.N.

from the ipsilateral or contralateral cerebellum but he did find two units projecting into the medial lemniscus which were trans-synaptically activated from the cerebellum. Not all the cells in the L.C.N. relay into the medial lemniscus as Grant and Westman (1969) saw cells remaining after section of the medial lemniscus. Non relay cells may be inhibitory interneurones as Fedina, Gordon and Lundberg (1968) have evidence of pre-and-post synaptic inhibition ascending in a crossed ventrolateral spinal tract.

In 1954 Grundfest and Carter reported a tract in the ipsilateral dorsolateral funiculus evoking potentials in the inferior olive. This tract crossed before the olive and was excited by cutaneous nerves. However Marchi techniques failed to show degeneration in the inferior olive after lesions in the dorsolateral funiculus. Kreiger and Grundfest (1956) showed that the tract contained a synapse in the L.C.N. Di Baggio and Grundfest (1956) found that this tract was inexcitable from the cerebellum and hence independent of the D.S.C.T. and Horrobin (1966) has shown, by collision, that collaterals of axons in the rostral medial lemniscus and originating from the L.C.N. reach the inferior olive. Thus the spino-olivary tract of Grundfest may be identical with the spino-cervical tract.

Lateral cervical nuclei have been found in a large number of species but the morphology and size of the nucleus varies. The following table lists some of these findings.

Cat	Rexed and Strom (1952)
Dog	Rexed (1958)
Sheep	"
Seal	"
Whale	"
Raccoon	Ha Kitai Morin (1965)
Elephant shrew	Ha Morin (1964)
Tree shrew	"
Lemur	"
Slow Loris	"
Galago	"
Capuchin monkey	"
Squirrel monkey	"
Macaca	"
Japanese monkey	Mizuno, Nakano, Imaizumi, Okamoto (1967)
Owl monkey	"
Rhesus monkey	Ha (1971)
Man	(a) 9 out of 10 specimens Truex, Taylor, Smythe and Gildenberg (1970)
Man	(b) Nauta technique Kircher and Ha (1968)

Reports have been made that lateral cervical nuclei are not present, or very rudimentary, in the potto (Ha and Morin, 1964), rabbit (Mizuno, 1966 and Brown, 1968b), rat, guinea-pig and man (Rexed, 1958). However there are contradictions in the literature concerning rodents. Gwyn and Waldron (1968, 1969) and Waldron (1969) have used a

cholinesterase stain to identify cells which they assume are homologous with lateral cervical nuclear cells. In the rat, guinea-pig, rabbit and hedgehog, they claim that the nucleus corresponds to a thin lamina of cells extending the length of the cord, in the ferret they found interrupted nuclei throughout the length of the cord whilst in the cat and monkey the nuclei, as expected, were found in the first two cervical segments (Rexed, 1954). They proposed that the number of cells in the S.C.T. was inversely proportional to motor skill and the number of axons in the dorsal column system. However no electrophysiological studies appear to have been made specifically on such units or their central projections. If they project to the thalamus it is possible that Dilly, Wall and Webster (1968) included such units in the rat's spinothalamic tract. Furthermore, there is no pharmacological evidence to support the assumption that acetylcholine is associated with the lateral cervical nucleus.

Andersson, Norssell and Norssell (1972) have suggested that the S.C.T. is less important in cynomologus monkeys than cats in eliciting short latency surface positive potentials in the somatosensory cortex following cutaneous stimulation; in this monkey a crossed ventral tract is involved. However their hypothesis may not be generally applicable to primates as Ha (1971) has shown that the rhesus monkey possesses a much better defined L.C.N. than many sub-primate species.

Grant and Westman (1969) and Westman (1969) have studied spinal afferents to the L.C.N. with Golgi, Nauta and electron-microscopical methods. Afferents enter the nucleus from all sides although the dorsal part of the lateral funiculus provides the majority of afferents; Westman confirmed Cajal's (1952) observation of afferent collaterals. Fibres tended to terminate in either large or small fields. Boutons en passant and boutons terminaux were visible. Three distinct types; those of spinal afferents, those of lateral cervical nuclear axon collaterals and those of interneurones were distinguishable. The most surprising finding of Westman was the sparcity of degenerating cells four days after cutting the lemniscal afferents; only 15% of the cells degenerated. Two years after the section a decrease in medium sized neurones and dendritic spines was observed. It is possible that some of these interneurones are inhibitory; there is evidence for both ascending (Fedina, Gordon, Lundberg, 1968) and descending (Peto, 1974) inhibitory actions on the nucleus.

Boivie (1970) has studied thalamic terminations after electrolytic lesions in the L.C.N. with Nauta techniques. He found, as did Busch (1961), that the lateral cervical nucleus sends its axons in the lateral part of the medial lemniscus and terminates in the lateral and medial nucleus ventro posterior lateralis, the medial posterior group of nuclei and the magocellular part of the medial geniculate. Terminations were most abundant in the nucleus postero-lateralis.

This agrees with the electrophysiological experiments of Landgren, Nordwall and Wengstrom (1965) and Andersen, Andersson and Landgren (1967). The former workers found that the spino-cervical projection surrounded "like a shell" the dorsal column nuclear projection to the nucleus ventro posterior lateralis and 20 of 62 units could be fired by the spino-cervical tract alone. The latter authors studied units excited by the spino-cervical tract which were "lateral" to those excited by dorsal column stimulation. Convergence from fore and hind limb and dorsal columns was observed. The S.C.T. typically gave large excitatory post-synaptic potentials (E.P.S.P.) and many S.C.T. relay cells could be antidromically excited from both the S.I. and S.II areas of the cerebral cortex, suggesting a bifurcating projection.

Methods of electrophysiological identification of S.C.T. axons or cell bodies should exclude spino-cerebellar fibres, and propriospinal fibres in the dorsolateral funiculus and should also demonstrate that the response to stimulation of peripheral nerves is both orthodromic and ascending, thus excluding axons conveying cutaneous information rostro-caudally in the D.L.F. as found by Dart (1971). A necessary and sufficient procedure of identification is:

(1) Antidromic activation from stimulating electrodes placed just below the L.C.N. on the dorsolateral funiculus of the third cervical segment. Collision of an antidromic action potential with an action potential elicited by natural or electrical stimulation of a peripheral nerve

will show that the cutaneous response is truly orthodromic and unless antidromically fired during the refractory period, ascending. Collision also eliminates fibres which are activated by antidromic impulses in dorsal column fibres. The technique of frequency following, used alone, is probably not sufficient as Albe-Féssard, Levante and Lamour (1974) have found units following thalamic stimulation rates of 200 - 300 Hz which do not collide with peripherally evoked impulses.

(2) Failure to activate antidromically from stimulating electrodes placed above the lateral cervical nucleus, or a significant slowing of the axon's conduction velocity bewteen the two pairs of stimulating electrodes. Brown and Franz (1969) included units whose conduction velocity between C.I and C.3 is 50% or less of that between C.3 and the recording site.

The destination of collaterals of S.C.T. axons in the L.C.N. is unknown and units included on this criterion need reinvestigation. The results of Randic, Mysinski and Gordon (1976) and Tapper, Mann, Brown and Cogdell (1975) seem to imply that such axons project to the cerebellum.

Although at lumbar levels a high proportion of axons in the superficial and medial part of the dorsolateral funiculus (D.L.F.) belong to the S.C.T. (Taub and Bishop, 1965; Brown, 1973) only a minority of dorsal horn cells project into the D.L.F. Fetz (1968) found that 43% of lamina IV and 19% of lamina V cells in the sixth lumbar segment could be antidromically fired from the D.L.F. of the fourth lumbar segment. Thus particular care should

be taken in the identification of the cells of origin of the S.C.T.

Much of the literature on the S.C.T. is open to the criticism that the units studied have not been rigorously identified. Some authors (Wall, 1960, 1965) have simply used antidromic activation from the D.L.F. of the lower thoracic cord, others have used exclusion of D.S.C.T. units (Lundberg and Oscarsson, 1961). Lundberg (1964), Taub and Bishop (1965) and Brown and Franz (1969) have used antidromic stimulating electrodes at C.I and C.3 to delineate the spino-cervical tract. None of these authors used collision techniques systematically.

Early workers on the spino-cervical tract found excitation from two tactile stimulus modalities; hair movement and pressure (Lundberg and Oscarsson, 1961; Wall, 1960; Taub, 1964; Taub and Bishop, 1965). In an attempt to correlate the responses of these second order axons more closely with those of primary afferents, Brown and Franz (1969) found that four types of spinocervical tract unit could be distinguished in decerebrate cats on the basis of mechanical stimulation.

Type I Excited by movement of tylotrich hairs

Type II Excited by movement of guard hairs and sometimes strong pressure

Type III Excited by all three types of hair and weakly excited by pressure

Type IV Had either no receptive field or were weakly excited by pressure.

Pacinian corpuscles, receptors in the glabrous skin of foot pads, both types of slowly adapting mechanoreceptors and claw receptors did not excite S.C.T. axons.

In the spinal state all types of hair excited S.C.T. units of Type I, II and III and pressure and temperature excited types II, III and IV. Gregor and Zimmermann (1972) showed with cathodal blockade that some dorsal horn neurones were excited by both the A and C waves of peripheral nerves and Brown, Hamann and Martin (1973) and Hamann (1974) showed by reversible D.C. polarisation that some S.C.T. fibres were excited by primary afferents with conduction velocities in the 'A' range whilst others were excited by primary afferents in both the 'A' and 'C' ranges. In general those S.C.T. axons excited by pressure and pinch had a 'C' fibre input. As in spinal preparations all types of S.C.T. units are excited by temperatures greater than $45^{o}C$. This must be due at least partially to activity in myelinated fibres.

Taub and Bishop (1965) claimed that only sural nerve fibres conducting in the Aδ range excited S.C.T. units. However tylotrich hair receptors have the largest primary afferent fibres in cutaneous nerves (Brown and Iggo, 1967) and these receptors do excite S.C.T. units. Unfortunately, because of the differential slowing of D.C. axons previously referred to, the fastest axons in the D.C. are from rapidly adapting receptors in the foot pads (Brown, 1968b, Petit and Burgess, 1968) which do not excite S.C.T. units (Taub, 1964; Brown and Franz, 1969). Pad receptors are not represented in the sural nerve and it is possible that

Taub and Bishop confused their massed electrical activity with that of hair units.

Receptive fields of S.C.T. units are continuous, circular or oval with the longer axis parallel to the longer axis of the limb. As is the case for primary afferents in adult cats (Brown and Iggo, 1967) and the cutaneous component of the D.S.C.T. (Mann, 1971)they tend to be smaller in the periphery and larger centrally (Taub, 1964; Taub and Bishop, 1965; Brown and Franz, 1969). Taub (1964) found that the size of the receptive field of S.C.T. axons could be reduced by stimulation of the brain stem, and Zieglgansberger and Herz (1971) induced increases in the receptive field of S.C.T. cell bodies by cooling the thoracic cord or by iontophoretic application of glutamate. However, Wall (1967) and Fetz (1968) failed to find descending influences on the sizes of receptive fields of cells in laminae IV and V and Brown (1971) found that only 3 out of 41 identified S.C.T. units changed their receptive fieldsize when the spinal cord of a decerebrate cat was blocked reversibly by cooling.

Estimates of the average conduction velocity of S.C.T. axons computed from the latency of units in the lumbar cord to antidromic stimulation of the cervical dorsolateral funiculus are surprisingly consistent at just under 60 ms^{-1}. Brown and Franz (1969) computed a mean of 59.5 ms^{-1} with a range of 17-103 ms^{-1} and Taub and Bishop (1965) using micropipettes as opposed to tungsten microelectrodes found a mean of 58.0 ms^{-1} with a more limited range of 46.0 - 88.0 ms^{-1}. The distribution of conduction velocities is

unimodal with a modal value of 66 - 72 $m\,s^{-1}$ but type II units have significantly lower conduction velocities than the other types. Spontaneous activity was more frequent in spinal than decerebrate and chloralose anaesthetised cats; units excited by pressure tended to have the highest rates of spontaneous discharge (Brown and Franz, 1969).

Thus in contrast to the dorsal columns, the conduction velocity of axons in the S.C.T. is greater than that of axons in peripheral nerves thus explaining the early observations that hind limb cutaneous activity in the D.L.F. reached high cervical levels 0.75 m.s. quicker than in the D.C. (Norsell and Voorhoeve, 1962) and that the latency of the cortical response evoked by stimulation of the hind limb was 3·0 m.s. shorter when evoked by the D.L.F. rather than the D.C. (Andersson, 1962). With fore limb stimulation Andersson (1962) found no significant latency difference but Oscarsson and Rosen (1966), also using barbiturate anaesthesia, found the dorsal columns to be the faster (by 0.8 m.s.) pathway from the superficial radial nerve.

Recently Whitehorn and co-workers, (Whitehorn, Morse and Towe 1969; Ennever and Towe, 1974) have questioned the importance of the S.C.T. in evoking short latency cortical potentials. They inserted a mica plate between the dorsal columns and dorsolateral funiculus in the spinal segments C.4 - C.5 and found that electrical stimulation of the D.L.F. only evoked potentials in the cortex when stimulation strengths were sufficient to spread to the dorsal columns.

They were also unable to evoke potentials from the superficial radial nerve in the absence of the dorsal columns. Andersson and Leissner (1975) repeated these experiments taking more care not to damage blood vessels and cells in the dorsal horn and using a Teflon plate for insulation. Their positive results are more acceptable as the published lesions of Whitehorn's group show considerable damage to dorsal horn cells which may contain S.C.T. cells activated by the S.R.N. Imai and Kusama (1969) showed that dorsal roots conveying primary afferents from the forepaw may extend as rostrally as C.4.

Cells of origin of the S.C.T. have been found in laminae III, IV, V and VI by the method of reconstruction of electrode tracks (Eccles, Eccles and Lundberg, 1960: Wall, 1960; Fetz, 1968, Bryan, Trevino, Coulter and Willis, 1973). In the hind limb most of these cells are in or adjacent to a segment containing their excitatory primary afferents (Willis, Weir, Skinner and Bryan, 1973). Intracellular iontophoresis of procion dyes and horseradish peroxidase have also been used to locate S.C.T. cells (Bryan, Trevino, Coulter and Willis, 1973; Brown, House and Hume, 1975; Snow, Rose and Brown, 1976; Jankowska, Rastad and Westman, 1976). Procion yellow M.4.R. and procion scarlet M.G. show S.C.T. cells at depths of 1200 to 2200μM from the cord dorsum. The dendritic fields of superficial cells extend to within 200μM of the tip of the dorsal horn and no correlation was found between either somatic volume and conduction velocity or depth in the

grey matter and physiological properties (Brown, House, Rose and Snow, 1975). This contrasts with the statement of Hillman and Wall (1969) that S.C.T. cells arising from lamina V "respond to a much wider range of pressure stimuli" than those in lamina IV. However caution should be exercised in the interpretation of procion stained material as Zieglgansberger and Reiter (1974) have evidence of interneuronal movement of procion yellow in dorsal horn neurones.

Intracellular staining with horseradish peroxidase offers several advantages over the procion method. The reaction product is electron dense and Jankowska, Rastad and Westman (1976) have observed lysozome-like organelles in electron-micrographs of monosynaptically excited S.C.T. cells containing this electron dense reaction product. Snow, Rose and Brown (1976) have made extensive light microscopical observations of S.C.T. cells stained with horseradish peroxidase. Axons in the D.L.F. are stained up to 25 mm away from the cell body (as opposed to 2 mm with procion) and axon collaterals which are rarely seen in procion stained material are visible. Furthermore, with the horseradish method, dendritic trees are more extensively stained; these appear to form a continuous sheet dorsal to the cells of origin of the S.C.T.

Hongo, Jankowska and Lundberg (1968) saw both excitatory and separate, reversible, inhibitory, post-synaptic potentials when recording from S.C.T. cells monosynaptically excited by electrical or natural stimulation. Price, Hull

and Buchwald (1971) have observed excitatory postsynaptic potentials followed by inhibitory postsynaptic potentials in cells in laminae IV to VI of spinal cats. Bessou, Catchlore, Fetz and Le Bars (1974) produced a block of excitability of lamina IV cells by depolarising them with the putative excitatory transmitter, glutamate, and found that this was reversible by stimulation of the cell's inhibitory receptive field.

Wall (1965) has proposed that action potentials originate in the dendrites of S.C.T. cells. He bases this hypothesis on an analysis of extracellular field potentials of orthodromic, antidromic and spontaneous dendritic activity and on the presence of spikes arising directly from the resting potential rather than from an excitatory post synaptic potential. Wall (1965) thought that it was "possible that all these recordings were taken from within axons". Some controversy exists as to the existence of such spikes arising from the baseline. Hongo, Jankowska and Lundberg (1968) deny their existence whilst Price, Hull and Buchwald (1971) have observed them. The recent results of Snow, Rose and Brown (1976) with the horseradish peroxidase technique further complicate this dispute as the dendritic trees may well be too long for electrotonic propogation to the soma.

Extracellular studies have shown that S.C.T. cells are subject to inhibition from a variety of sources. The presence of inhibition is largely dependant on the state of the preparation (Brown and Franz, 1969) and the type of

anaesthetic used (Brown and Short, 1974). Early workers Wall (1960), Eccles, Eccles and Lundberg(1960), Lundberg and Oscarsson (1961) failed to observe inhibitory receptive fields for S.C.T. cells. Taub (1964), Taub and Bishop (1965) and Brown and Franz (1969) observed inhibitory receptive fields. Inhibitory receptive fields do not appear to be the exclusive domain of a particular type of receptor although Brown, Hamann and Martin (1973) showed that "C" fibres could only excite S.C.T. cells. However inhibitory receptive fields for S.C.T. axons may be found on the ipsilateral or contralateral limb or trunk (Brown and Franz, 1969). In gracile neurones inhibitory receptive fields are often found surrounding excitatory ones (Gordon and Jukes, 1964).

Recently (Tomasulo and Emmers, 1970; Davidson and Smith, 1970; Dart and Gordon, 1970, 1973) it has been shown electrophysiologically that, in both the cat and rat, afferent fibres excite the dorsal column nuclei after section of the dorsal columns. Gordon and Grant (1972) have shown degeneration with the Fink-Heimer method in the dorsal column nuclei after section of the dorso lateral funiculus.

In the gracile and cuneate nuclei of the cat, cells are both excited and inhibited by natural stimulation of ipsilateral and contralateral cutaneous receptive fields when the dorsal columns are cut. Their afferent fibres ascend in the dorsolateral funiculus and do not project to the cerebellum (Dart and Gordon, 1973). Thus some of

them may be collaterals of S.C.T. axons.

Dart (1971) has also observed cells in the dorsal column nuclei with axons descending in the D.L.F. and suggested that they inhibit S.C.T. cells. Brown and Martin (1973) could not corroborate this hypothesis as section of the brain stem just rostral to the dorsal column nuclei removed the inhibition on S.C.T. axons elicitable by orthodromic volleys in the dorsal columns.

These findings illustrate that tracts ascending in the dorsal columns and dorsolateral funiculi may be functionally interdependant. As has been pointed out (Gordon, 1973) this possibility makes the interpretation of behavioural observations on animals with lesions in the dorsal part of the spinal cord very difficult.

Many workers have studied behavioural changes after spinal cord ablations and there is considerable controversy on the subject. Sherrington (1900) cites Schiff's result that after cutting all of the spinal cord, except for the dorsal columns, rabbits may be alerted by tactile stimulation below the level of the lesion. Wall (1970) could find no evidence for this in rats. Tapper (1970) trained cats to respond to mechanical stimulation of S.A.I touch receptors. This response survived dorsal column section and may be dependent on the integrity of the dorsal spino-cerebellar tract (Mann, 1971). Schwartzman and Bogdanoff (1969) found rhesus monkeys sensitive to vibration after dorsal column lesions. Kitai and Weinberg (1968) found that ablation of the dorsolateral but not the

dorsal columns affected roughness discrimination in cats and Norssell (1966) found that sectioning both dorsal and dorsolateral columns affected conditioned reflexes to air puffs on the hind leg of the dog. Kennard (1954) produced hyperalgaesia in cats by injections of alumina cream and could only prevent pain responses by cutting the dorsolateral funiculus.

Thus behavioural experiments have failed to provide an unequivocal answer to the question of whether there is functional localisation within the spinal cord. The complexity of the interconnections between the ascending paths (Gordon, 1973), the plasticity of the relay nuclei (Miller, Basbaum and Wall, 1976) and different methods of evaluating sensory deficits may all be partly responsible for this.

7. The forelimb component of the spino-cervical tract.

Relatively little is known about the fore limb component of the S.C.T. Its existence has been inferred from cortical potentials evoked in contralateral S.I and S.II and ipsilateral S.II by a tract ascending in the ipsilateral dorsolateral funiculus (Catalano and Lamarche, 1957; Mark and Steiner, 1958; Norssell and Voorhoeve, 1962; Andersson, 1962; Andersson and Leisner, 1975). Holmqvist, Oscarsson and Uddenberg (1963) and Holmqvist and Oscarsson (1963) studied evoked waves in dissected fasciculi of the spinal cord. They found that in the third cervical segment ipsilateral tracts, activated monosynaptically from forelimb nerves, occupied the dorsal two thirds of the lateral funiculus whilst below the cervical enlargement they occupied only the dorsal third. They concluded that there was a forelimb component of the spino-cervical tract. Taub (1964) demonstrated that tetanization of the contralateral superficial radial nerve inhibited hind limb S.C.T. cells. However he did not state if this result was obtained in decerebrate or spinal cats.

As previously mentioned there are marked differences in the forelimb and hind limb components of the afferent tracks to the cerebellum and dorsal column nuclei. Thus it is pertinent to ask if this is also true for afferents to the lateral cervical nucleus. Furthermore little is known about limb-limb interactions on sensory spinal neurones.

8. The control of transmission through ascending sensory systems.

The concept of descending inhibition of "muscular tonus" was used by Sherrington (1906) to explain the effects on ocular muscles of Faradic stimulation of the cerebral cortex. Brouwer (1933) proposed descending inhibition of sensory input and Hagbarth and Kerr (1954) showed that ascending massed activity in sensory paths could be attenuated by stimulating higher centres. Dawson (1958) pointed out that this could be partly an occlusive effect and Hagbarth and Fex (1959) and Jabbur and Towe (1959) showed that single sensory units could be both excited and inhibited by stimulating more rostral parts of the brain.

Although descending control is regarded as being a very important phenomenon in cutaneous sensory mechanisms its function or functions are by no means clear. Hernández-Péon (1959) suggested the concept of centrifugal influences modulating attention and this is a particularly attractive idea when considering the reticular formation. Eccles (1964) proposed that descending inhibition acted as a negative feedback mechanism controlling further afferent input. This explanation is difficult to reconcile with the finding that massed lemniscal activity evoked from the forelimb diminishes about 150 m.s. prior to voluntary movement in the cat (Ghez and Lenzi, 1970; Coulter, 1974).

None of these hypotheses can at present fully explain the phenomenon of the mutual presynaptic inhibitory actions of primary afferents. Direct evidence for this has been

obtained by Eccles, Magni and Willis (1962) who recorded from inside presynaptic fibres. Due to the technical difficulties of intra-axonal recording indirect evidence for presynaptic inhibition is more common in the literature. This may include some or all of the following.

(1) 'p' wave, a positive deflection of the cord dorsum potential (C.D.P.) following a short initial negative wave (Gasser and Graham, 1933; Bernhard, 1953).

(2) The negative dorsal root potential (D.R.P.) with the same time course as the positive cord dorsum potential (Barron and Matthews, 1938).

(3) Increased excitability, as measured by the relative electrical threshold, of primary afferent terminals (Wall, 1958).

(4) Picrotoxin diminishes D.R.P.'s (Eccles, Schmidt and Willis, 1963b).

(5) Antidromic discharges in dorsal roots (Schmidt, 1971).

Primary afferent depolarisation (P.A.D.) of hind limb mechanoreceptors exhibits a surround type of topographical organisation (Schmidt, Senges and Zimmerman, 1967b). Jänig, Schmidt and Zimmerman (1968b) showed that rapidly and slowly adapting mechanoreceptors exert P.A.D. preferentially on themselves and this was regarded as a negative feedback mechanism. P.A.D. may also be elicited by noxious stimuli (Vyklicky, Rudomin, Zajak and Burke, 1969). Single primary afferents from pad mechanoreceptors do not exert a P.A.D. on themselves (Jänig, Schmidt and Zimmerman, 1968 a, b).

Mendell and Wall (1964) have reported positive dorsal

root potentials following electrical stimulation of C fibres. In non-spinal preparations it is dubious whether this phenomenon is a true primary afferent hyperpolarisation or disinhibition (Lundberg, 1964 (Wall's paper); Lundberg and Vylicky, 1966; Hongo, Jankowska and Lundberg, 1972). For spinal cats there are contradictions in the literature concerning the sign of dorsal root potentials following C fibre stimulation. Franz and Iggo (1968), Zimmermann (1968) and Janig and Zimmermann (1971) found that C fibre inputs were followed by negative D.R.P.'s.

Melzack and Wall (1965) proposed a gate theory to explain certain aspects of pain. It was suggested that cells transmitting pain were facilitated by ongoing activity in small afferent fibres which were in turn inhibited by fibres with a larger diameter. The gate theory has been very influential among psychologists and neurologists (Nathan, 1976) but requires re-evaluation in the light of the neurophysiological experiments which it has stimulated (Wall, 1973).

Electrical stimulation of the brain stem (Carpenter, Engberg and Lundberg, 1966; Wall, 1967; Hongo, Jankowska and Lundberg, 1972) and cortical areas S.I and S.II (Andersen, Eccles and Sears, 1962; Lundberg, Norrsell and Voorhoeve, 1963; Carpenter, Lundberg and Norrsell, 1963) can modulate P.A.D. and D.R.P.'s.Both facilitatory and depressive effects have been seen after stimulation of the brain stem but it is also possible that the interneurones eliciting presynaptic inhibition are themselves

presynaptically inhibited as stimulation of the brain stem may prevent or reverse the sign of D.R.P.'s elicited by primary afferents (Lundberg and Vylicky, 1966). An alternative explanation is that tonic and phasic descending actions are brought about by different interneurones.

It is difficult to determine which tracts are responsible for the descending control of presynaptic inhibition of either primary afferent fibres or interneurones. The reasons for this are two-fold: firstly, the location of the cells producing presynaptic inhibition is disputed. Even if it were known it would be difficult to show that the cell under study was producing presynaptic inhibition, and secondly, there is the problem of electrically stimulating one descending tract in isolation.

Thus many of the descending tracts are thought likely to exert descending control of P.A.D. and little is known about their individual differences.

Negative D.R.P.'s have been observed after stimulating the pyramidal tract (Carpenter, Lundberg and Norrsell, 1962; Fetz, 1968). However, negative D.R.P.'s may also be elicited by stimulating the sensorimotor cortex of pyramidotomised cats (Hongo and Jankowska, 1967) and hence stimulating the sensorimotor cortex should not be regarded as exciting the cortico-spinal tract exclusively.

Other pathways involved may include (1) the rubrospinal tract; Hongo, Jankowska and Lundberg (1972) could modify D.R.P.'s by stimulating the red nucleus; (2) the reticulo spinal tract; this may also be involved in the tonic

inhibition found in S.C.T units in decerebrate preparations (Brown and Franz, 1969) as the most rostral section needed to release flexor reflex afferents from tonic inhibition is at low pontine levels (Carpenter, Engberg, Funkenstein and Lundberg, 1963).

Inhibitory post-synaptic potentials within S.C.T. cells are short (Hongo, Jankowska and Lundberg, 1968) and cannot account for more than the first 40 m.s. of the 200 m.s. inhibition from non-excitatory segmental sources reported by Brown and Kirk (1972). Thus a presynaptic inhibitory mechanism may be at work, as suggested previously by Eccles, Kostyuk and Schmidt (1962).

If it is assumed that the cord dorsum 'P' wave reflects the dorsal root potential (Barron and Matthews, 1938) then it is reasonable to propose that the inhibition in S.C.T. cells evoked from both descending and segmental systems is partially due to presynaptic inhibition of primary afferent fibres. However, a number of experimental observations are difficult to reconcile with this hypothesis.

(1) S.C.T. cells do not have the "surround inhibition" seen in primary afferent depolarisations (Schmidt, Senges and Zimmermann, 1967b).

(2) S.C.T. units in spinal cats excited solely by rapidly adapting hair receptors could not be inhibited by stimulation of hairs but only by pressure or squeezing (Brown, 1968b). This may be contrary to Jänig, Schmidt and Zimmermann's observation that rapidly adapting afferents preferentially depolarise the terminals of other rapidly

adapting afferents.

(3) A pure 'C' fibre volley produces a negative dorsal root potential (Zimmermann, 1968) but 'C' fibres do not inhibit S.C.T. cells (Brown, Hamann and Martin, 1975).

(4) Both barbiturate and chloralose potentiate the presynaptic inhibition of primary afferents (Schmidt, 1964) but the segmental inhibition of S.C.T. cells may be absent in barbiturate anaesthetised preparations (Lundberg and Oscarsson, 1961) and is suppressed by chloralose (Brown and Franz, 1969). Brown and Short (1974) demonstrated in chloralose anaesthetised cats, that the inhibition elicited by stimulating the sensorimotor cortex was labile to barbiturate.

(5) The first action potential of a monosynaptically activated S.C.T. cell may not be delayed by conditioning stimuli (Brown, Kirk and Martin, 1972).

Thus use of the cord dorsum potential as evidence of a presynaptic inhibitory mechanism on S.C.T. cells is not altogether satisfactory.

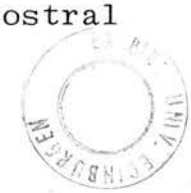
When investigating descending inhibitory influences on ascending systems it is necessary to consider whether the descending inhibition is acting directly on the cell under study or its afferents. Thus Peto (1974) felt obliged to cut the dorsolateral funiculus when investigating cortico-fugal effects upon the lateral cervical nucleus. Similarly it is plausible that descending effects on S.C.T. cells are due at least in part to inhibition of inter-neurones providing, among other functions, a polysynaptic

input to S.C.T. cells. Hence it is important to draw the distinction between descending inhibition of spino-cervical tract cells and the descending inhibition of transmission through the spino-cervical tract.

Wall (1967) and Brown (1970,1971) showed that reversible cold block of the thoracic spinal cord released tonic inhibition of S.C.T. units in cats decerebrated at the level of the colliculi. Descending systems originating in the mid-brain, hindbrain or cervical enlargement could be responsible for this. Brown and Franz (1969) found units in high spinal cats similar to those in the reversible preparations and so the brain stem exerts a tonic inhibition on the S.C.T.

Taub (1964) showed by electrical stimulation that the S.C.T. could be inhibited from the mesencephalic tegmentum, cerebellar nuclei and the central pontobulbar core. Lundberg, Norrsell and Voorhoeve (1963) failed to inhibit the S.C.T. from the cerebral cortex and similarly Wall (1967) could not inhibit lamina IV cells by stimulating the pyramids. Fetz (1968) demonstrated pyramidal inhibition on lamina IV cells and Brown and Short (1974) found that stimulation of the contralateral hind limb areas of S.I and S.II inhibited the S.C.T.

Brown, Kirk and Martin (1973) stimulated the spinal cord segments C2-C4 with tungsten microelectrodes and found that inhibition of hind limb units could be elicited bilaterally in both the dorsolateral and ventral funiculi and by stimulation of the dorsal columns when cut rostral



to both the recording and stimulating electrodes. This latter effect could be due to vestibulospinal fibres which are known to be present in the cervical dorsal columns (Erulkar, Sprague, Whitsel, Dogan and Jannetta, 1966).

Thus the corticospinal, rubrospinal, vestibulospinal and reticulospinal tracts are all possible sources of descending inhibition on transmission through the S.C.T. Brown, Kirk and Martin (1972) have proposed that the descending tracts share interneurones with segmental inhibitory fibres as there are no obvious quantitative or qualitative differences between the two sources of inhibition and occlusion may be demonstrated between them.

9. The Sensorimotor Cortex and Corticofugal Inhibition.

In 1870 Fritsch and Hitzig (translated von Bonin 1960) demonstrated that by electrical stimulation of the anterior part of the dog's cerebral cortex "one obtains combined muscular contractions of the opposite side of the body". Five centres were specified in constant loci for the muscles of the neck, the extensors and abductors of the anterior leg, flexion and rotation of the same leg, the posterior leg and the facial muscles. The concept of localisation of motor function was advanced by Ferrier (1875) in lower apes and Leyton and Sherrington (1917) in anthropoid apes. These authors found the motor cortex anterior to the central sulcus, and encompassing area 4 and the adjacent part of area 6 of Brodmann (1909). However there was no particular tendency to follow the cyto-architectural pattern. They also drew attention to the instability of the effects of electrical stimulation and analysed them into three components; facilitation, deviation and reversal.

On the grounds of the sensations produced by electrical stimulation of human brains (Bartholow, 1874; Cushing, 1909) and the sensory deficits of patients with cerebral lesions (Bergmark, 1909) it was thought that the sensory cortex was posterior to the motor cortex. Corroborative evidence for this hypothesis was gained by observing sensory deficits in monkeys following localised ablations or the application of strychnine sulphate (Dusser de Barenne, 1916, 1924). These methods revealed a crude

contralateral topographical representation, with the leg represented medial to the arm.

The use of amplifiers and oscilloscopes to record cortical potentials evoked by near threshold mechanical stimuli, with known temporal and spatial parameters, revealed detailed topographical maps of the somaesthetic cortex (Bard, 1937-1938). In the monkey which has a clearly defined central sulcus the sensory representation was found posterior to this sulcus (Marshall, Woolsey and Bard, 1941; Haynes and Woolsey, 1944) but the general mediolateral hind limb and forelimb arrangement was similar. A second bilateral representation was found by Adrian (1940, 1941) in the cat and he suggested it was peculiar to this species. Woolsey (1946, 1947), however, showed it was also present in the rabbit, sheep, pig and monkey and suggested it had a motor function. The two representations are conventionally distinguished chronologically as S.I and S.II. In some species (cat and rabbit) potentials are evoked in S.II before S.I whilst in others (pig and monkey) the reverse occurs (Woolsey, 1947). Visceral afferents also project to the somato-sensory cortex of cats and monkeys and occupy the same area as the trunk (Downman, 1951; Amassian, 1951).

Marshall, Woolsey and Bard (1941) found that the fore-foot of the cat elicited short latency surface positive potentials in three areas of the cortex. Darian-Smith, Isbister, Mok and Yokota (1966) have suggested that the face and forelimb are represented topographically in

triplicate in chloralose anaesthetised cats. Single units in S.III had longer latencies to forepaw stimulation (10.35 m.s. v.s. 8.63 m.s.) than those in S.I and S.II but were unaffected by cooling S.I and S.II. Their receptive fields were sometimes large, bilateral or excited by auditory stimuli; barbiturate diminished receptive field sizes.

Darian-Smith's S.III is situated either just rostral or caudal to the ansate sulcus depending on whether it is continuous with the coronal sulcus. Oscarsson and Rosén (1966) have studied the projection of cutaneous receptors in the cat's S.R.N. to the cortex when either the D.C. or S.C.T. are cut. In both pathways cutaneous afferents projected to two areas corresponding to Darian-Smith's S.I and S.III. However Oscarsson and Rosén (1966) regarded S.I as being part of the motor cortex and S.III as being sensory cortex. The D.L.F. gave larger amplitude potentials and extended more rostrally in S.I., and the D.C. transmitted larger and more widespread potentials to S.III. Both groups of workers noted that hind limb afferents did not have a dual representation but Oscarsson and Rosén (1966) thought this was due to a hidden projection in the cruciate sulcus.

Thus there appears to be a discrepancy in the literature concerning the extent of the feline sensory and motor cortices. Livingston and Phillips (1957) used surface stimulation to delineate the cat's motor cortex and found that, in the same hemisphere, the receiving and motor areas were largely coextensive, the only major difference being

that the forelimb receiving area was larger and sometimes extended into the hind limb motor area.

Surface stimulation has obvious disadvantages when considering the geometry of the cerebral sulci. Delago (1952) demonstrated, by stimulating with insulated needle electrodes, that part of the hind limb motor cortex was hidden within the cruciate sulcus and that part of the forelimb, neck and face cortex was in the presylvian sulcus. The former findings have recently been confirmed by Nieoullon and Rispal-Padel (1976) by controlled stimulation (30, 300 Hz., 0.5 m.s., 100μA pulses applied through varnished nickel chrome electrodes) in awake cats. Their results also agree with the cytoarchitectural map of Hassler and Muhs-Clement (1964) who found that the motor cortex was largely rostral to the postcruciate dimple. Area 6 was found to control more axial parts of the musculature whilst area 4 controlled limb musculature.

Atkinson, Seguin and Weisendanger (1974) could only find evidence of motor effects from S.II when it was stimulated in depth with currents strengths six to ten times greater than those which elicited movements from the first sensory motor cortex. They concluded that the corticospinal projection from S.II which has been demonstrated anatomically by Nyberg-Hansen (1969) was involved in the corticofugal control of afferent input rather than in motor function as proposed by Woolsey (1947) and Garol (1942).

The current strength needed to elicit movements from the surface of the cat's motor cortex is one or two orders

of magnitude greater than that sufficient in peripheral nerves. Thus a critical approach to the effects of cortical surface stimulation is essential. Phillips (1956 a, b) recorded intracellularly from Betz cells and stimulated the motor cortex with a monopolar ball electrode. He found that discharges in single Betz cells at low frequency were insufficient to provoke movement. For single 10 m.s. rectangular pulses the movement threshold ranged from 0.5 to 1.5 m.A. Whilst the threshold for single cells ranged from 25 to over 250 μA depending on their depth from the surface. Currents exceeding 100 μA were needed to provoke high frequency firing of Betz cells and single surface positive (anodal) pulses were more effective than surface negative (cathodal) in stimulating Betz cells. Hence when cathodal pulses are more effective in eliciting Betz cells it is possible that they are acting indirectly through more superficial internuncials. Phillips estimated that Betz cells were excited within a 5 mm radius of the electrode at current strengths near threshold for movement. Thus surface stimulation is a relatively imprecise method of locally stimulating the pyramidal tract.

An alternative means of exciting Betz cells is to stimulate through micro-electrodes. This offers the advantages of being able to record unit activity and of stimulating a small, precisely defined area of cortex with a high local current density. Asanuma and Sakata (1967) and Stoney, Thompson and Asanuma (1968) have used glass

insulated tungsten micro-electrodes for intracortical microstimulation (I.C.M.S.).

Such electrodes are of high impedance and thus the current passed through them is in the micro ampere range. A disadvantage of this type of micro-electrode is electrolytic etching of the tungsten tip which occurs when cathodal pulses are used. This affects both the recording characteristics and the current density contours surrounding the tip when it is used for I.C.M.S. Jankowska, Padel and Tanaka (1975 a, b) have successfully used 3 MΩ Na.Cl. filled micropipettes with 2.0 - 2.5 μM. tip diameters for I.C.M.S.

Stoney, Thompson and Asanuma (1968) repeated Phillip's (1956 a,b) experimental paradigm using I.C.M.S. rather than surface stimulation. They found that Betz cell thresholds could be as low as 1μA cathodal (or 3μA anodal) and estimated that for a 10μA 0.2 m.s. pulse 30 Betz cells were stimulated. Asanuma, Stoney and Abzug (1968) studied the relationship between input and output with I.C.M.S.; stimulating with 11 pulses of 0.2 m.sec. duration at 2.5 m s intervals, in the region of the postcruciate dimple, which elicits movements of the forelimb at thresholds as low as 1.4μA (cathodal), they found that the cutaneous receptive field of neurones within a given efferent zone were most frequently found on a skin region that lies in the pathway of the limb movement produced by stimulating in that area.

Although these studies have shown that Betz cells may be excited directly by very low currents they do not exclude the possibility that the motor effects are the result of excited fibres trans-synaptic influences. The long trains of pulses typically used by Asanuma et al. would certainly favour this.

Jankowska, Padel and Tanaka (1975 a,b) have most elegantly investigated this possibility by comparing anti- and orthodromic latencies of single pyramidal tract cells recorded from and stimulated in the motor cortex and dissected lateral fascicles of the spinal cord. Using signal averaging to detect the orthodromic spike in the spinal cord they found that 'orthodromic' latencies were in two thirds of the units 0.3 m.s. or more longer than antidromic latencies. This time lag is consistent with synaptic excitation of Betz cells as is the observation that pulse trains were more efficient in causing delays. Investigating the monosynaptic excitatory post synaptic potentials, found in monkey motoneurones after stimulating the pyramidal tract, Jankowska, Padel and Tanaka (1975b) found that I.C.M.S. with current strengths of 2-3 μA excited only one motor neurone species whilst current strengths of 5-10μA excited two or more motor neurone species. Direct activation of pyramidal tract cells with surface stimulation was associated with a 'D' wave component in the descending volley.

Thus I.C.M.S. should not be used uncritically in attempts to locate areas of the cortex from which sensory or

motor corticofugal effects may be elicited. Such localisation may be acceptably deduced if it can be shown that all the fibres stimulated run tangentially to the cortical surface. There is some anatomical and good physiological evidence for such a columnar arrangement (Mountcastle, 1957; Powell and Mountcastle, 1959 a,b; Globus and Scheibel, 1967; Werner and Whitsel, 1968; Hubel and Weisel, 1969; Grant, Landgren and Silfvenius, 1975). Mountcastle (1957) studied receptive fields of neurones in the anaesthetised cat's first and second somaesthetic cortex. Cells responded to one of three types of stimuli, hair movement, pressure on the skin, or stimulation of deeper lying receptors; muscle stretch was not an effective stimulus; receptive fields were similar at all depths of electrode penetrations normal to the surface and there was no continuous relationship between depth and latency. Thus Mountcastle proposed a columnar organisation of receptive fields. In the post-cruciate dimple area Mountcastle found a predominance of deep receptors. Oscarsson and Rosén (1966) demonstrated that Gp.I muscle afferents from the forelimb do project to the post cruciate dimple area, and Landgren and Silfvenius (1969) found a double hind limb Gp.I muscle afferent representation more medially in area 3A.

The functional properties of cells in S.II have been investigated by Carreras and Andersson (1963) and Andersson (1962). No modality specificity was observed, receptive fields were sometimes discontinuous and large and nociceptive receptive fields, particularly in the posterior region of S.II,

were more common than in S.I. Joint movement was not found to be an effective stimulus.

In barbiturate anaesthetised cats with either the dorsal or dorsolateral columns sectioned, Andersson (1962) saw units with small distal receptive fields. Inhibitory receptive fields were only observed in cats with intact dorsal columns.

Jones and Powell (1969) showed with the Nauta technique that lesions in the ventrobasal complex cause degeneration in both S.I and S.II and this degeneration is somatotopically organised particularly in S.I. However they found no projection rostral to area 3A and thus the more rostral area of short latency potential found by Oscarsson and Rosen (1966) to follow stimulation of the superficial radial nerve with cut dorsal columns may relay elsewhere. Manson (1969) found by antidromic identification that one half of the ventrobasal complex neurones project to both S.I and S.II whilst the remainder project only to S.I. The projection of the posterior group (P.O.) of thalamic nuclei is less certain; Andersson (1962) and Poggio and Mountcastle (1960) suggested that they were responsible for the wide and nociceptive fields in S.II, a suggestion reminiscent of the protopathic system of Head and Sherren (1905). Rowe and Sessle (1968) found cells in the P.O. nuclei which could be antidromically excited from both S.I. and S.II and Heath and Jones (1971) found axonal degeneration in a continuous band of insular and suprasylvian cortex following lesions in the P.O. nuclei. However this

area did not include S.II or S.I. Calma (1965) showed that P.O. neurones received afferents via tracts in the D.C. The D.L.F. and the ventral cord and that complex inhibitory interactions were present. Curry (1971) found most cells in the P.O. nuclei had cutaneous hair receptive fields and very few were nociceptive. He also found that cells were antidromically excitable from either S.I or S.II. Thus the function of the posterior group of thalamic nuclei may not be compatible with the earlier speculations of Poggio and Mountcastle (1960).

Jones and Powell (1973) have classified cortical interconnections as intrinsic association, extrinsic association and interhemispheric. The former are ipsilateral and reciprocally interconnect S.I and S.II and certain regions within S.I and S.II. The extrinsic association connections link both S.I and S.II with the motor and supplementary motor cortices and S.I to area 5 (association cortex) (Jones and Powell, 1968). Inter-hemispheric connections link S.I with contralateral S.I and S.II and S.II with the contralateral S.II only (Jones and Powell, 1968). With the ordinary Nauta techniques only the axial areas appear to be interconnected but with the Fink-Heimer modification interconnections are seen between the distal extremities (Shanks, Rockel and Powell, 1975). Innocenti, Manzoni and Spidalieri (1972)have recorded intracellularlyfrom neurones in S.I and S.II with trans-callosal influences. They typically have wide bilateral receptive fields, 81% were excited and 19% inhibited from

the opposite hemisphere. As expected neurones in S.I received effects only from contralateral S.I whilst neurones in S.II were influenced from both S.I and S.II. The neurones receiving effects were scattered throughout the cortex but most were in the axial projection region. Innocenti, Manzoni and Spidalieri (1974) further studied the receptive field properties of axons in the rostral part of the corpus callosum. They were arranged somatotopically and all had lemniscal type receptive fields; the majority being on the face. Thus it was proposed that the corpus callosum linked midline areas of both hemispheres.

Corticofugal fibres have been demonstrated anatomically in the cat by Kuypers (1960); Kawana and Kusama (1964) and Kawana (1969) and Nyberg-Hansen (1969). Recently the horseradish peroxidase method has been used to label antidromically such corticofugal cell bodies (Coulter, Ewing and Carter, 1976). Such fibres end in the dorsal and ventral horn and originate from both S.I and S.II.

Gordon and Miller (1969) have identified the location of corticofugal fibres projecting to the dorsal column nuclei by stimulating their axons in these nuclei and recording the antidromic responses of individual cell bodies in the cortex. Cortico-gracile neurones were found medially and cortico cuneate neurones laterally. Histological examination of electrolytic lesions made at the recording site revealed that they were all in area 3a of Hassler and Muhs-Clement (1964). Recently it was proposed that some of the recording sites were in the adjoining areas 4_γ and 3b

(Brown, Coulter, Rose, Short and Snow, 1975). The cells studied by Gordon and Miller (1969) did not project into the spinal cord and thus it is possible that the spino-cervical tract is inhibited by a sepratae set of cortico-spinal fibres.

Brown and Short (1974) found that both the contralateral hind limb cortical receiving areas inhibited hind limb S.C.T. axons at a stimulus voltage which did not give rise to such inhibition elsewhere in the sensorimotor cortex. Brown, Coulter, Rose, Short, Snow (1975) repeated the experiment using I.C.M.S. to condition the responses of S.C.T. somata to electrical stimulation of peripheral nerves. Trains of 3, 400 Hz. 10-15μA pulses were effective inhibitory stimuli in certain loci in areas 3b, 3a and 4γ . These loci could be bracketed by electrode tracks which did not give inhibition suggesting a discrete localisation of cortico-fugal elements.

Peto (1974) has used I.C.M.S. to define the cortical areas which inhibit the lateral cervical nucleus. He found that the facial area was most effective and that natural stimulation of the face was a very potent source of inhibition on L.C.N. cells. This is of interest as Brown and Short (1974) found that the face area could also inhibit S.C.T. axons at a reasonably low stimulus intensity and Wall and Taub (1962) have evidence of a trigeminal projection to the L.C.N.

Thus it would be of interest to know if the forelimb receiving area inhibits S.C.T. cells activated by forelimb

cutaneous afferents. Furthermore it is not known whether the ipsilateral cortex can also inhibit the S.C.T. Recently Cole and Gordon (1976) showed that the cortico-fugal inhibition of cells in the cuneate nucleus had a shorter time to peak than that of cells in the gracile nucleus. Whether a similar phenomenon occurs for S.C.T. units is unknown.

Anaesthetics

Anaesthetics present an obvious problem to studies of somaesthetic function and it has been shown that many anaesthetics including barbiturates, volatile and aliphatic anaesthetics and urethane affect both the mechanisms of presynaptic inhibition (Schmidt, 1964) and the transmission of cortical evoked potentials (Derbyshire, Rempel, Forbes and Lambert, 1936; Marshall, Woolsey and Bard, 1941).

Nembutal prolongs the recovery rate and decreases the spontaneous activity of cortical evoked potentials. Marshall (1941) suggested that the effect on the recovery rate occurred in nucleus ventro posterior lateralis of the thalamus. Woolsey (1947) states that deep barbiturate anaesthesia is a "necessary condition for obtaining more or less purely monophasic responses" and criticises Adrian's (1940) discovery of the second somatosensory cortex as "due to an unfavourable state of anaesthesia"; Adrian (1940) used the convulsive anaesthetic chloralose and urethane. Hence many experiments on cortical evoked potentials are performed under deliberately deep barbiturate anaesthesia (60 m.g./k.g. or more intravenously). Downman (1951) found that a mixture of barbiturate and chloralose gave the best results.

This procedure is not altogether satisfactory for evoked potential studies, as Amassian (1954) showed that the somaesthetic association area could be demonstrated with chloralose but not barbiturate anaesthesia. For single unit studies tranquillising or light doses of

barbiturate (3 - 20 m.g/k.g. intravenously (Asanuma, Stoney and Abzug, 1968; Heath, Hore and Phillips, 1976), chloralose (Innocenti, Manzoni and Spidalieri, 1972) or ketamine (Atkinson, Seguin and Weisendanger, 1974) are the anaesthetics of choice as large doses of barbiturate may impede synaptic transmission. Experimental results on cortical cells obtained without general anaesthesia can show marked differences to those obtained with anaesthesia (Duffy and Burchfiel, 1971).

Barbiturates and chloralose increase the amplitude of dorsal root potentials (Lloyd, 1952; Schmidt, 1963). Initially the time course of D.R.P. is shortened but after a few minutes it increases so that for the purposes of general anaesthesia both chloralose and barbiturate must be regarded as potentiating primary afferent depolarisation (Schmidt, 1964). Anaesthetics may also potentiate primary afferent depolarisation by indirect mechanisms such as lowering the blood pressure or body temperature. Toennies (1939) showed that the dorsal root reflex was most easily demonstrable by synchronous volleys in cold preparations.

Neuromuscular blocking agents are also known to affect synaptic transmission. Galindo, Krnjević and Schwartz (1968) showed that Flaxedil applied either systemically or iontophoretically could excite cells in the cuneate nucleus; 'hair cells' were particularly vulnerable.

Section II

Receptive Fields and Conduction Velocities of Identified Spinocervical Tract Axons in the cervical spinal cord.

INTRODUCTION

In Section I it was contended that the properties of spino-cervical tract units with somata in the lumbosacral cord could be adequately described as excited by a limited part of the previously described hind limb primary afferent receptor population. The experiments described in this Section were designed to answer three questions:

(1) Is there an electrophysiologically definable component of the spino-cervical tract receiving an afferent input from the forelimbs?

(2) If so, are spino-cervical tract units activated by forelimb afferents qualitatively similar to their counterparts in the lumbosacral cord?

(3) Are there any quantitative differences in conduction velocity or unit types between spinocervical tract units activated from different parts of the body?

In particular it was hoped that an analysis of the properties of units of different types and receptive field locations might yield a clue as to how the spinocervical system copes with events occurring at different parts of the body but at the same time.

METHODS

Surgical Techniques

The experiments were performed on 22 cats of both sexes and weighing 1.8 - 3.2 kg. Anaesthesia was induced with a mixture of 4% Halothane in 50% oxygen and 50% nitrous oxide applied through a face mask. The skin covering the throat was shaved and a mid-line incision made in the skin through which it was possible to dissect both carotid arteries and one external jugular vein from their surrounding connective tissue. Care was taken to avoid damage to the Vagus nerve. One carotid artery was cannulated for monitoring blood pressure and the other ligated. One of the jugular veins was also cannulated to facilitate intravenous injection. The trachea was then cleared of connective tissue and cannulated with a polythene Y tube through which the cat was anaesthetised until the decerebration was completed. The throat incision was closed either with sutures or metal clips and the cat was righted with its head secured in a clamp.

The hairs of the head were then shaved and a rostro-caudal incision of about 3 cm. in length was made slightly to the left of the midline. A hole of 1.5 cm. diameter was trephined in the cat's skull to the left of the central suture. The dura mater was cut and whilst the anterior vertebral arteries were temporarily occluded by an assistant the brain was sucked out until the colliculi were visible. The cortex rostral to the bony tentorium was then removed with the aid of a spatula and the skull was filled with

cotton gauze moistened with 0.9%saline. To prevent further bleeding from the wounds bone wax was applied to the skull and surgical gauze to the sectioned ends of the brain stem. The skin wound was closed with metal clips and the animal inspected for the signs of decerebrate rigidity (Sherrington 1906).

The hairs from the atlanto-occipital joint to T4 were shaved in the midline; care was taken to preserve as much of the trunk hair as possible for later natural stimulation. The spinal cord was then exposed by laminectomy between C1 and T2. Careful dissection with scissors along the midline aponeurosis of the muscles of the back of the neck was efficacious in minimising bleeding. When this did occur it was stopped with 0.9% saline moistened Steripson, bone wax or arterial forceps. During the laminectomy and subsequently the animal was paralysed with gallamine triethiodide (Flaxedil) and artificially ventilated with intermittent positive pressure ventilation (20 x 35-55 cc./min.) This prevented damage to the spinal cord which might be caused by reflex movements. The dura mater was then cut and reflected along the entire length of the laminectomy and the spinal cord kept moist with cotton gauze soaked in 0.9% saline. A bilateral pneumothorax was performed and kept patent with polythene tubes inserted between the ribs. This helped to decrease respiratory movements whilst recording. The superficial radial nerves were exposed two thirds of the way down each forearm and freed from the cephalic vein with nerve hooks made from glass rods. Care was taken to avoid undue damage to the

skin of the forearm. The medial plantar nerves were exposed in the plantar aspect of the feet and freed from the flexor retinaculum with nerve hooks. All four nerves were then kept moist with cotton wool moistened with 0.9% saline.

The cat was then transferred to a rigid table and supported in a stereotaxic head holder (Clark and Ramsay, 1975) and frame by means of clamps on two thoracic and one lumbar vertebrae and bars in the roof of the mouth, the medial rostral maxilla, and both external auditory meatuses.

On the ventral surface of the cat was a thermostatically controlled electric blanket which was set to maintain a rectal temperature of 38°C. The expired air was analysed by a Grubbs-Parsons CO_2 meter and the respiratory volume adjusted to maintain a constant expired CO_2 level of 3.8 - 4.5%. A continuous record was kept of the blood pressure and if the diastolic pressure fell below 60 mm.Hg. a mixture of equal volumes of 4% 40,000 and 6% 110,000 molecular weight Dextrans solutions (both in 0.9% saline) was administered.

The skin and muscle overlying the cervical cord were reflected with sutures tied to the frame. A long silver wire was placed in the exposed neck muscle and connected to earth and liquid paraffin was poured into the pool surrounding the exposed spinal cord. The four limbs were then attached to the frame by Gypsona plaster of Paris bandages and the dissected nerves were placed on bipolar hook stimulating electrodes made of chlorided silver wire. A paraffin wax mixture of melting point 45°C was poured over the exposed nerves to prevent dehydration.

Stimulating Techniques

A Devices Digitimer electronic time clock with trigger and gate facilities was used to trigger the oscilloscope and after variable delays to lead gating pulses to a pulse generator which determined the output of an isolated stimulator.

Recording Techniques

Mass potentials were recorded from the cord dorsum with a silver ball electrode. These potentials were led to a calibration box by a wire shielded to earth and thence to a Tektronix 122 pre-amplifier with frequency cut offs at 0.2 Hz. and 1kHz. and finally to a Tektronix 565 dual time base oscilloscope where they were displayed.

Unitary potentials ranging from about 200μV to 20mV, were recorded with tungsten micro-electrodes (Hubel, 1957) and led via an E.L.S.A. negative capacitance amplifier to another Tektronix 122 pre-amplifier, with cut off frequencies of 80 Hz. and 10 kHz, and thence to the other beam of the Tektronix 565 oscilloscope. An Ampex PR 500 F.M. tape recorder was used to record these potentials which could be photographed later. An audio-amplifier and loudspeaker were connected to the Y axis output of the oscilloscope to monitor potentials during the experiment.

Recordings were made from axons at or near the surface of the medial part of the dorsolateral funiculus in the segments C4-C5. The respiratory and cardiovascular movements present in the cervical spinal cord made it difficult to

hold axons for longer than 5 - 10 minutes. Ventral flexion of the head and slight stretching of the neck were found to increase stability and small balls of saline moistened cotton wool were placed between the dura mater and the medial surface of the spinal column to dampen movements. On two occasions Agar Agar, 4% weight for weight in 0.9% saline, was applied at 40°C to diminish cord movement but it was difficult to see through and the spinal cord appeared ischaemic when it was removed.

Identification of spino-cervical tract axons

Two pairs of bipolar ball stimulating electrodes were placed on the dorsolateral funiculus at C1 and C3 with their cathodes caudal. Blood and saline were regularly sucked off the surface of the spinal cord to prevent irregular spread of stimulating current and at the end of the experiment the distances between the pairs of stimulating electrodes and the recording electrode were measured with a piece of cotton fibre placed on the cord. Square wave pulses of 0.2 m.s. duration were led from an isolated stimulator to a junction box and thence to the stimulating electrodes on the dorsolateral funiculus.

The dorsal columns were not cut caudal to the spinal segment C3 as the recording site was between the spinal segments C4 and C5 and such a section would have decreased recording stability. Furthermore the consequent ischaemia and haemolysis of red blood cells would have damaged the spino-cervical tract neurones, particularly those with cell

bodies in the cervical region.

The recording micro-electrode was driven through the spinal cord by a stepping motor attached to a control unit made in the Department of Veterinary Physiology (Clark and Ramsay, 1975). This allowed the depth and speed of the electrode's descent to be monitored. Only the most superficial 800μm of the dorsolateral funiculus was sampled. The electrode typically entered between the C4 and C5 dorsal roots so as to sample as wide a range of receptive fields as possible. It was driven at an angle of 10^{o} to 20^{o} to the vertical and towards the centre of the spinal cord.

Single units were considered to belong to the spino-cervical tract if there was no antidromic response from the C1 stimulating electrode or if there was a decrease in conduction velocity of 50% or more between C1 and C3. This method is similar to that used by Brown (1968b).

Mechanical stimulation of hairs and skin

Receptive fields of spino-cervical tract units were investigated by stroking the skin with a fine camel hair brush and by applying pressure with a small metal sprung clip. When time permitted the hair around the receptive field was cut with scissors and the receptive field examined under a binocular operating microscope with a fine blunt glass probe and a pair of watchmakers' forceps. No tests were made for temperature sensitivity. The application of the metal clip was considered to be

nociceptive. The extent of the receptive fields were sketched on figurines at the time of identification.

Movements of the metatarsal phalangeal and metacarpal phalangeal joints, the claws, foot pads and carpal hairs of Nilsson and Skoglund (1965) were performed when a receptive field encroached on these structures.

The term "slowly adapting" as used in this thesis implies an increased rate of discharge of a unit after a metal clip has been applied to its receptive field for 30 seconds. Rapidly adapting implies that no such increase is seen.

Results

The excitatory receptive fields of 247 identified spino-cervical tract units were investigated. All of the receptive fields were ipsilateral to the site of the recording micro-electrode; 12 of the fields on the trunk and tail had a small proportion of their surface area on the contralateral side.

43 units exhibited a spontaneous discharge but this was not observed in the other units. Where a spontaneous discharge was present "excitation" refers to an increase in discharge rate above the spontaneous rate.

Movement of carpal hairs, claws, touch corpuscles and pads, in isolation, were never observed to excite units. Five types of unit were distinguished on the basis of their response, or lack of response, to movement of hair, pressure and pinch of the skin, both hair movement and

Table 3

This summarises the qualitative experimental data of the results of Section II. The types of unit encountered in the 22 experiments are arranged in chronological order of the experiments from which they were drawn and are enumerated in terms of their receptive field type and location.

The types of unit were categorised as:

H	Responding to brushing of hairs only.
H & P	Responding to brushing of hairs and the application of a sprung metal clip.
P	Reponding to pinch or pressure only.
No	No receptive field could be found for these units.
J	Responding to movement, especially dorsiflexion of the metacarpal and metatarsal phalangeal joints.
Tail base	Responding to squeezing the base of the tail.

		FORELIMB					TRUNK				HINDLIMB				
Experiment	Total	H	H+P	P	NO	J	H	H+P	P	Tail Base	H	H+P	P	NO	J
7325	14	5	1	0	0	0	1	1	0	1	3	2	0	0	0
7326	5	0	0	0	3	0	0	0	0	1	0	0	1	0	0
7327	9	5	2	0	1	0	0	0	0	0	0	0	1	0	0
7328	32	6	1	0	3	0	3	2	0	2	5	8	1	0	1
7403	3	2	0	0	0	0	0	0	0	0	1	0	0	0	0
7404	4	1	2	0	0	0	1	0	0	0	0	0	0	0	0
7405	7	2	0	0	2	0	0	1	0	1	0	1	0	0	0
7406	7	3	1	1	0	0	1	0	0	0	1	0	0	0	0
7407	25	4	2	1	1	0	8	0	0	0	1	4	0	0	4
7408	11	3	2	0	1	0	0	0	0	1	1	1	1	0	1
7409	7	0	2	1	0	0	0	1	0	0	2	1	0	0	0
7410	2	0	2	0	0	0	0	0	0	0	0	0	0	0	0
7411	17	4	2	0	0	0	0	1	0	0	3	7	0	0	0
7412	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0
7413	15	1	2	0	0	1	2	1	0	0	2	5	0	0	1
7420	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0
7423	6	0	2	1	1	0	0	1	0	0	0	0	0	0	1
7425	11	1	3	1	0	0	1	0	0	0	1	2	2	0	0
7426	16	6	5	1	0	0	0	1	0	0	0	1	1	0	1
7427	21	5	5	1	2	0	2	1	0	0	1	2	2	0	0
7428	18	3	2	1	1	0	1	3	0	0	0	7	0	0	0
7429	12	1	7	0	0	0	0	0	0	1	0	2	1	0	0
Total	247	55	45	8	15	1	20	13	0	7	21	43	10	0	9
%	100	22.3	18.2	3.2	6.1	0.4	8.1	5.3	0	2.8	8.5	17.4	4.0	0	3.6
		50.2%					16.2%				33.6%				

pressure and movement of the metatarsal phalangeal joints.

Units excited by movement of hairs alone

This type accounted for 38.9% of the sample (96 units) and constituted the second largest single group of units. They responded with a rapidly adapting discharge to movement of large pigmented hairs and did not give a sustained discharge when a clip was placed on the receptive field.

Twenty one such receptive fields were examined in greater detail under the binocular dissecting microscope and all but one were observed to have punctate receptive fields. In 15 receptive fields touch corpuscles could be seen associated with the follicles of the excitatory hairs. These hairs were considered to be similar to the tylotrich hairs described by Straile (1960). One unit was found on the forelimb with no touch corpuscles in the vicinity of the excitatory hairs and it was concluded that this unit was excited by guard hairs (Straile, 1960) as the coloured hairs exciting it were not distributed in a punctate fashion.

There was considerable variation in receptive field size (Figure I). Those more distally situated tended to be smaller, often encompassing only one or two digits, whilst those on the trunk were never this small and often exceeded 30 cm^2 in area. Receptive fields were round or oval with their long axis parallel to the long axis of the limb; they were continuously circumscribed and no unit was found to have more than one receptive field. There

was a preponderance of units with receptive fields in the extremities. Both ventral and dorsal aspects of the limbs were represented. It was impossible to examine the ventral aspect of the trunk adequately.

Units excited by hair movement and pressure

These constituted 40.9% of the sample (101 units) and were the largest single group. They were identified by two criteria;

(1) excitation by brushing hairs with a fine brush, a rapidly adapting response;

(2) a slowly adapting response to pressure applied to the receptive field with a clip.

Twenty five such units were observed under the binocular microscope and in no case was isolated movement of a touch corpuscle or its associated hair follicle an effective stimulus. The small, fine, colourless Down hairs (Straile, 1960) were seen to excite these units as well as guard hairs. Because of the large size of some of the receptive fields it is difficult to state categorically that tylotrich hairs were not excitatory but this was never observed.

As with the hair only units the receptive fields were well circumscribed, most numerous distally and showed a proximal-distal decrease in receptive field size. The whole receptive field was excited by both hair and pressure; areas where only one stimulus was effective could not be found. Figure 2 shows receptive fields of this type.

Units excited by pressure or pinch

These units constituted 10.1% of the sample (25 units) and were found exclusively on the limbs (18 units) or the base of the tail (7 units). They could be excited by a clip to which they responded with a slowly adapting discharge but were more effectively excited by stronger pinch. Such units were probably nociceptive. Hair movement was never an adequate stimulus.

Unlike Hair only and Hair and pressure units there was no tendency for the proximal receptive fields to be larger. The largest receptive field was 16 cm^2 in area; most were much smaller than this and situated on the toes. The receptive fields were well circumscribed but because of the large degrees of displacement of skin needed it was difficult to determine if they were punctate or not. Investigation with sharp probes was not carried out for fear of damaging the receptive fields of other units. Unlike similar units reported in spinal cats (Brown, 1968b) no after-discharge was seen when the stimulus was removed. Figure 3 shows receptive fields of this type.

Units responding to movement of joints

These units accounted for 4% of the sample. Nine units were on the hind limb and one on the forelimb. All were excited by movement of the metatarsal - or metacarpal - phalangeal joints; dorsiflexion being more effective than plantarflexion. Manual pressure applied to the joint was also excitatory but evoked fewer impulses. Hair movement

or light touch with a glass probe to the opposing surfaces was not excitatory.

The response of these units was rapidly adapting and no spontaneous discharge was seen. Three of the hind limb units were excited by stimulating the medial plantar nerve. The forelimb unit could not be excited from the superficial radial nerve. It is posssible that these units were excited by afferent fibres from joint or muscle.

Units with no identified receptive fields

These constituted 6.1% of the sample (15 units) and were identified on the criteria of having no forelimb receptive field but were excited by stimulation of the superficial radial nerve. It is possible that these units were:

(1) units whose receptive field was damaged during dissection of the superficial radial nerve or whose afferent nerve fibres were interrupted. However all were taken from experiments in which receptive fields were present in the area supplied by the superficial radial nerve.

(2) high threshold units whose discharges were inhibited in the decerebrate state. This has been postulated by Brown (1968b).

(3) units with receptive fields in inaccessible places on the cat and for which the area supplied by the superficial radial nerve when naturally stimulated contributed to a subliminal fringe.

Figure 1

The excitatory receptive fields of the 21 hair only units examined under the dissecting microscope.

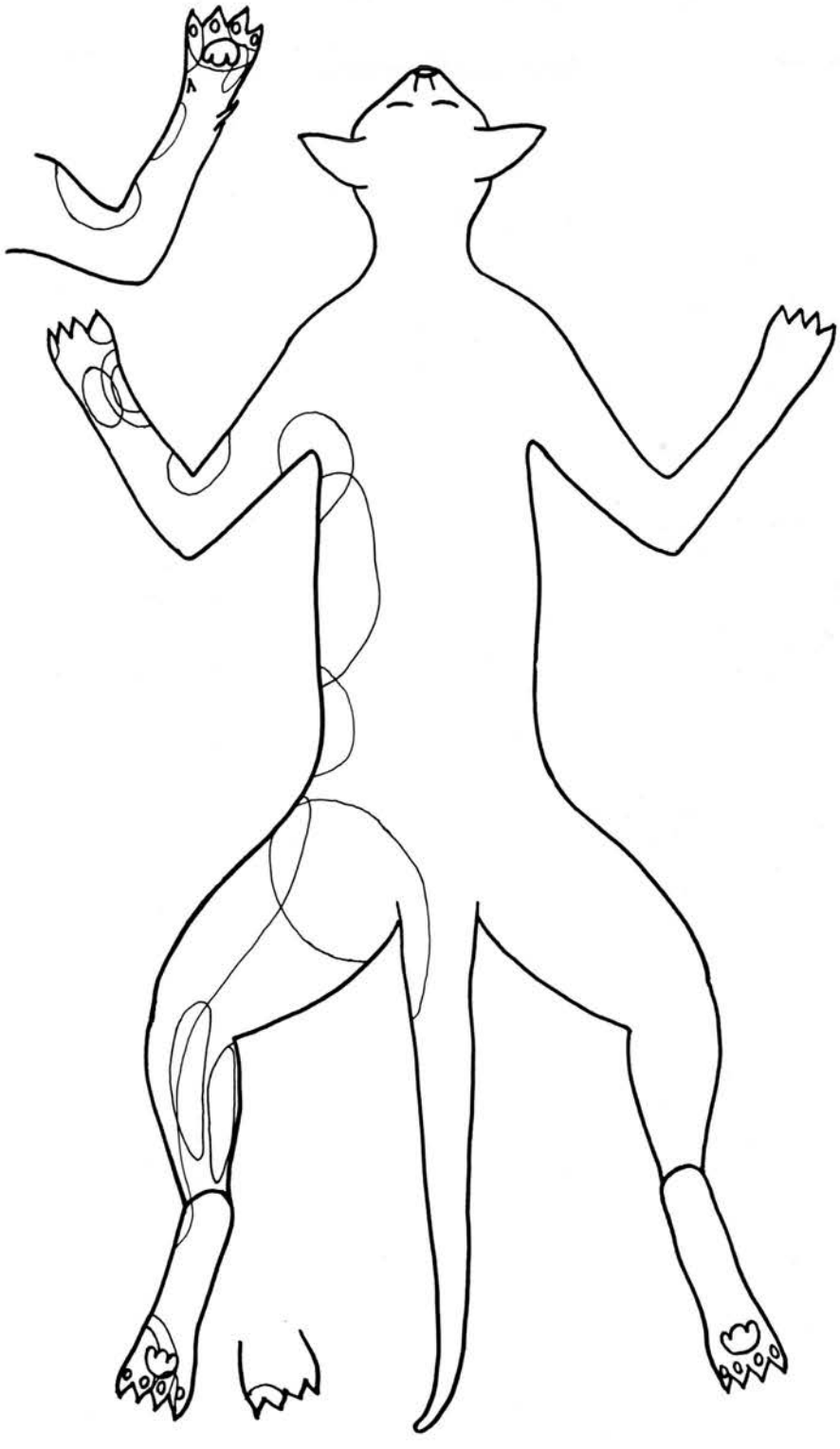


Figure 2

The excitatory receptive fields of the 28 hair and pressure units examined under the dissecting microscope.

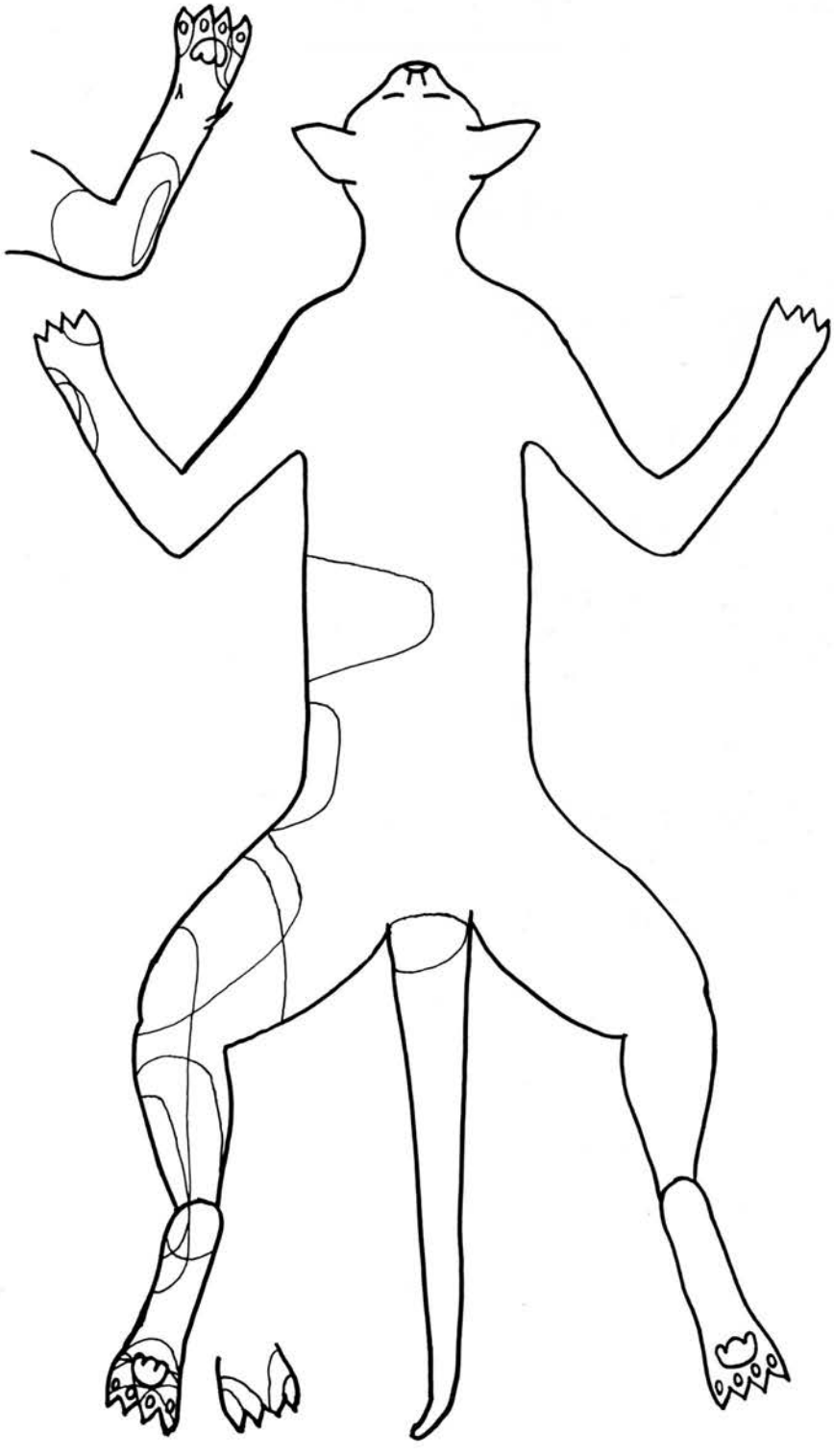
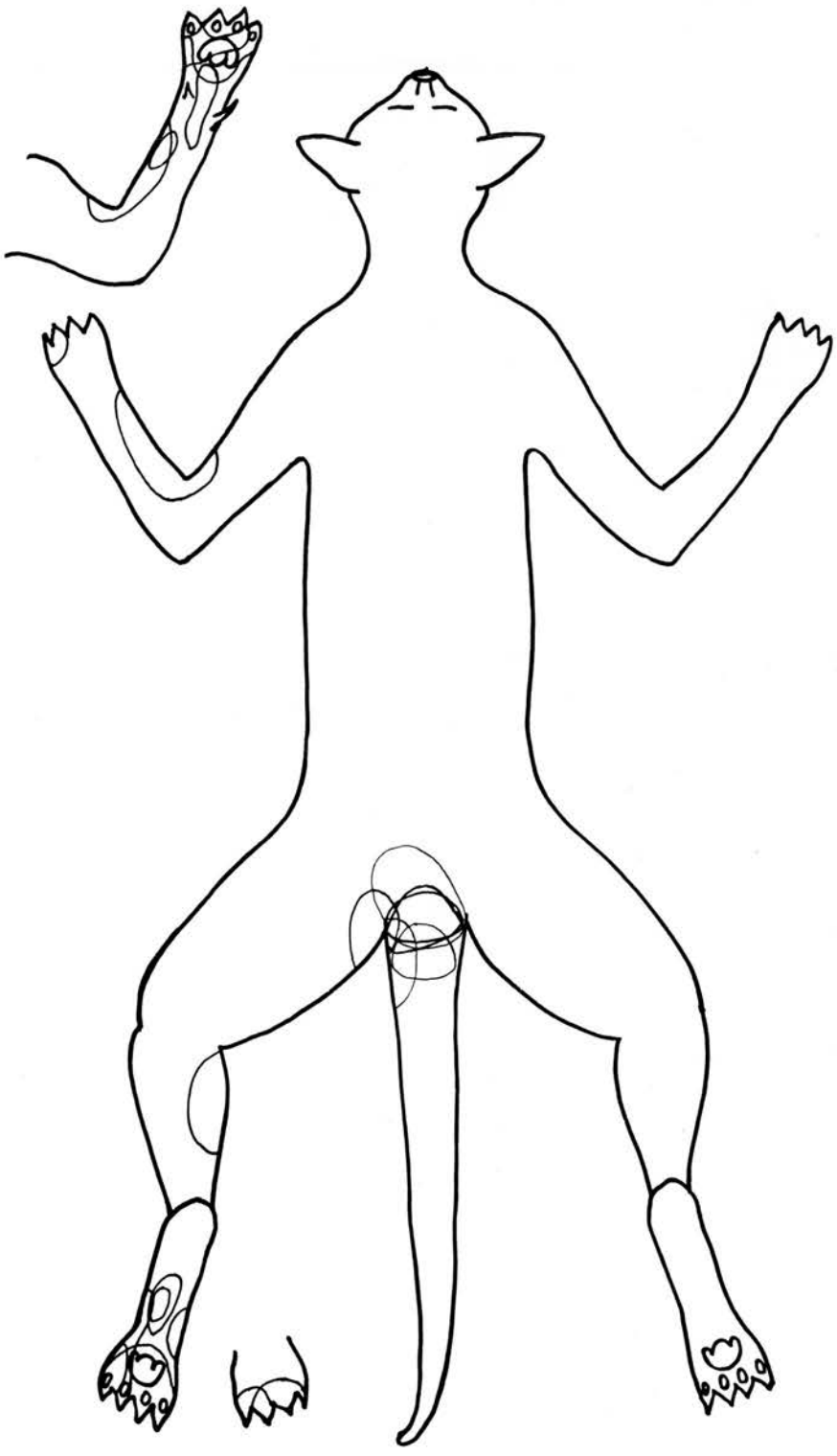


Figure 3

The excitatory receptive fields of the 25 units excited by pressure or pinch.



Quantitative differences in unit types between the hind limb, trunk and forelimb components of the spino-cervical tract.

Units excited by receptive fields in the forelimb accounted for 50.2% of the sample, those in the trunk 16.2% and those on the hind limb 33.6%. This corresponds to a ratio of 1:0·32 :0.67. As can be seen from Table 3 there was considerable variation in the ratios of forelimb to hind limb units in different experiments and it was thus important to discover if the difference was significant. A χ^2 test (Brandt and Snedecor's formula, cited in Fisher, 1963) revealed $P<0.07$. Thus the difference may be regarded as being moderately significant.

The other major difference between forelimb and hind limb was the larger proportion of hair only units in the forelimb component. This type of unit accounted for 44% of the forelimb component but only for 25% of the hind limb component. A Students t test was used to compare the difference in the ratios of forelimb hair to other types of forelimb unit and hind limb hair to other types of hind limb units. This was only done for the 12 experiments in which 9 or more units were sampled. The mean of the difference of the ratios was 0.96 and this difference was significant ($P<0.01$).

There have been no reports in the literature that the spino-cervical tract displays any form of topographical organisation of its axons. However as the tract has not previously been studied at cervical levels and as the differences in receptive field numbers in the forelimb and

hind limb could be due to biased sampling a scatter diagram of the recorded depths of units below the surface of the cord and their receptive field location was drawn (Figure 4). This shows that forelimb and hind limb units were randomly sampled within the spino-cervical tract. However no attempt was made to sample systematically the medio-lateral distribution of units and thus it is possible that topographical organisation exists in this dimension.

Conduction velocity of SCT axons in the cervical spinal cord.

The conduction velocities of axons were calculated from the latency of the rising phase of the antidromic spike timed from the beginning of the 0.2 ms square wave stimulation pulse applied at C3. The conduction distance was measured at the end of each experiment, and varied between 2.0 and 4.6 c.m. Thus in calculating the conduction velocity a small error in the numerator would lead to a sizeable percentage error.

The calculated range of conduction velocities was 12-110 ms^{-1}. They were unimodally distributed around a mean of 47.4 ms^{-1}, with a standard deviation of 21.1. The conduction velocities of the whole sample and of the individual unit types are displayed as a histogram in Figures 5 and 6.

As stated in the introduction it was of interest to know if the conduction velocities of spino-cervical tract axons were related to their receptive field locations. For a preliminary analysis of this question the receptive

Figure 4

The recorded depths below the surface of the spinal cord of 48 SCT axons from 6 experiments is plotted against the location of the excitatory receptive field.

The recordings were made between the C4 and C5 dorsal roots. The micro-electrode was driven into the dorsolateral funiculus at an angle of 10 - 20^{o} to the vertical and towards the centre of the spinal cord. The entry of the micro-electrode into the white matter was observed under the operating microscope and the micro-drive depth reading was zeroed.

The mean depth was 233.2 µm range, 10-450 µm, standard deviation 116.7.

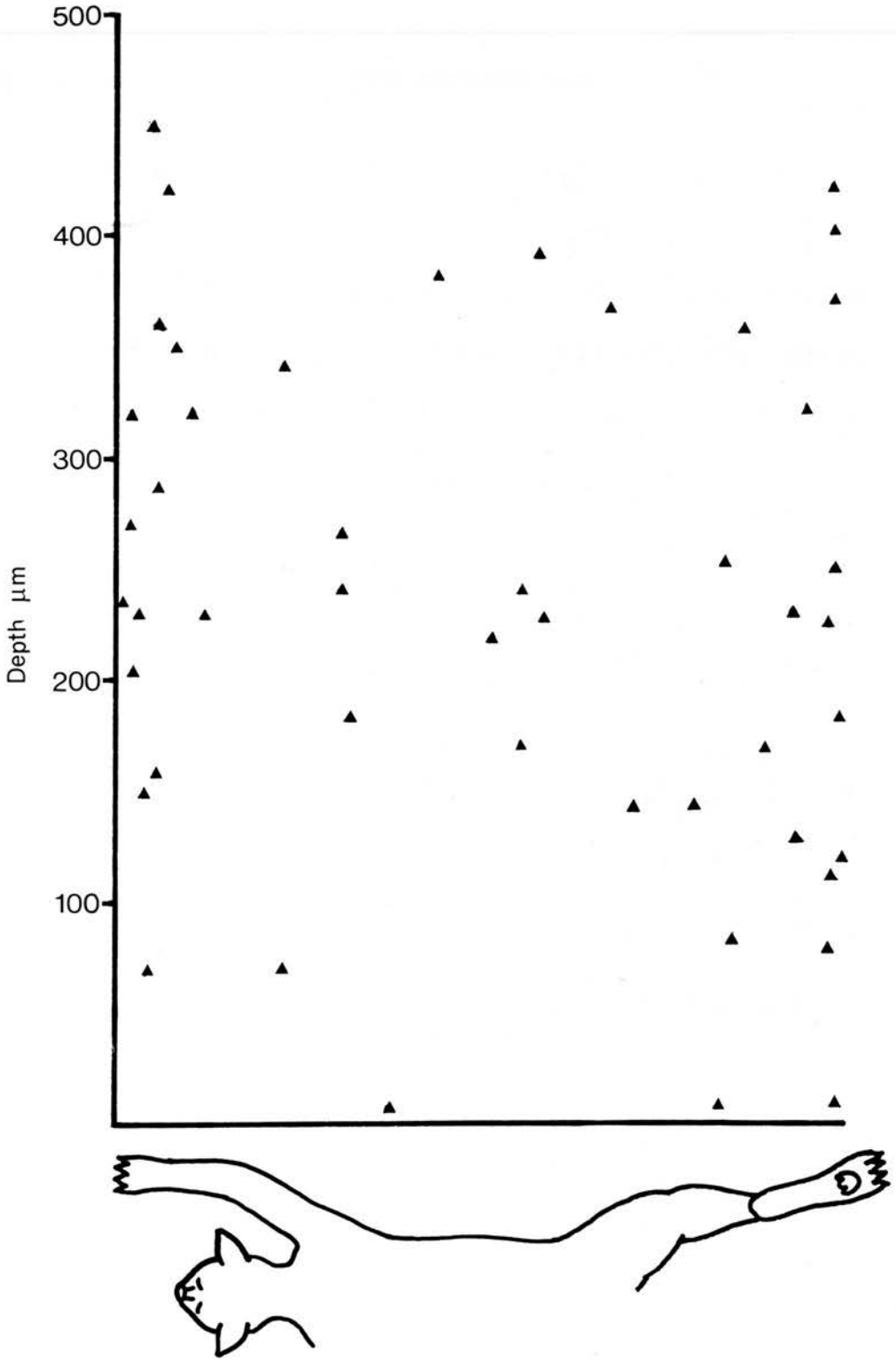

500
400
300
200
100
Depth µm

Figure 5

The conduction velocity histogram of 247 SCT axons. The velocities were calculated from the latency and distance travelled by the antidromic action potential elicited by stimulating the dorsolateral funiculus at C3. The mean conduction velocity was 47.4 ms^{-1} with a range of 12-110 ms^{-1} and a standard deviation of 21.1.

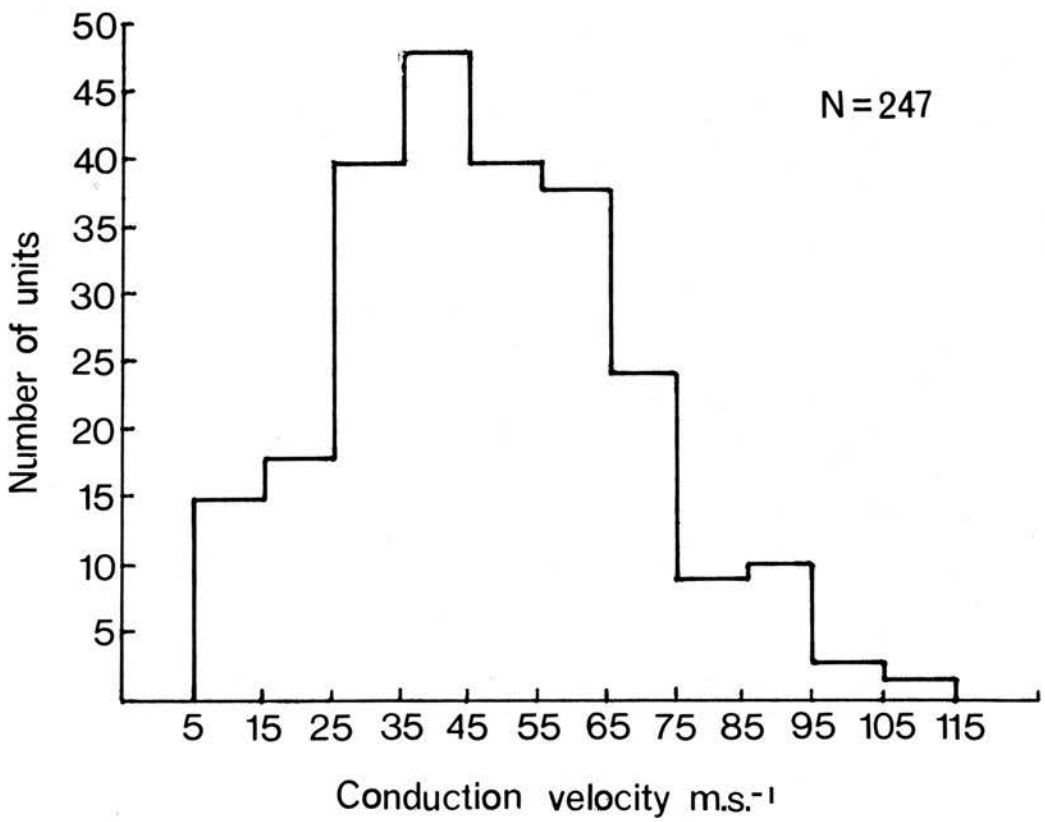

50
45
40
35
30
25
20
15
10
5
Number of units
N = 247
5
15
25
35
45
55
65
75
85
95
105
115
Conduction velocity m.s.-1

Figure 6

The conduction velocity histograms of the identified types of unit with receptive fields in the forelimb, trunk and hind limb.

	mean ms^{-1}	Range ms^{-1}	Standard Deviation
Base of tail pressure	41.6	12-70	20.5
Forelimb joint	35.0	-	0
No Receptive field	37.5	13-68	20.3
Forelimb pressure	40.1	20-62	17.8
Forelimb hair & pressure	48.6	13-94	18.5
Forelimb hair	44.8	12-92	21.2
Trunk hair	54.1	14-110	27.2
Trunk hair & pressure	52.1	22-101	26.5
Hindlimb joint	59.7	28-89	23.5
Hind limb pressure	44.2	14-90	21.7
Hind limb hair & pressure	48.1	13-109	18.8
Hind limb hair	49.6	21-93	19.5

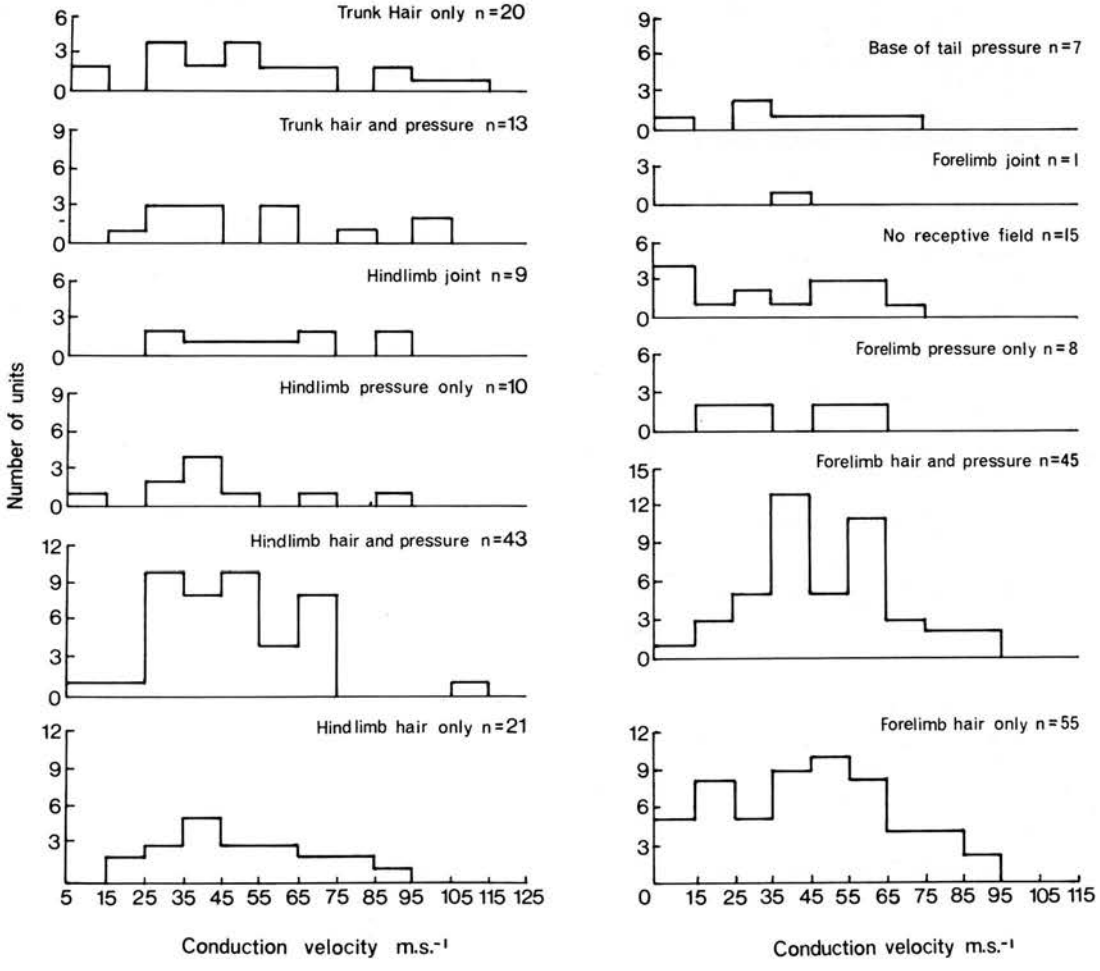

Trunk Hair only n=20
Trunk hair and pressure n=13
Hindlimb joint n=9
Hindlimb pressure only n=10
Hindlimb hair and pressure n=43
Hindlimb hair only n=21
Number of units
5 15 25 35 45 55 65 75 85 95 105 115 125
Conduction velocity m.s.-1
Base of tail pressure n=7
Forelimb joint n=1
No receptive field n=15
Forelimb pressure only n=8
Forelimb hair and pressure n=45
Forelimb hair only n=55
0 15 25 35 45 55 65 75 85 95 105 115
Conduction velocity m.s.-1

Figure 7

These histograms illustrate:

A The numbers of units with receptive fields on the forelimb, trunk and hind limb.

B The relative numbers of Hair only, Hair and Pressure, Pressure only and Joint movement unit types on the forelimb trunk and hind limb.

C This re-arrangement of the data of histogram B shows more clearly the dominance of Hair only units in the forelimb component and of hair and pressure units in the hind limb component of the SCT. Note the separate key for histogram C.

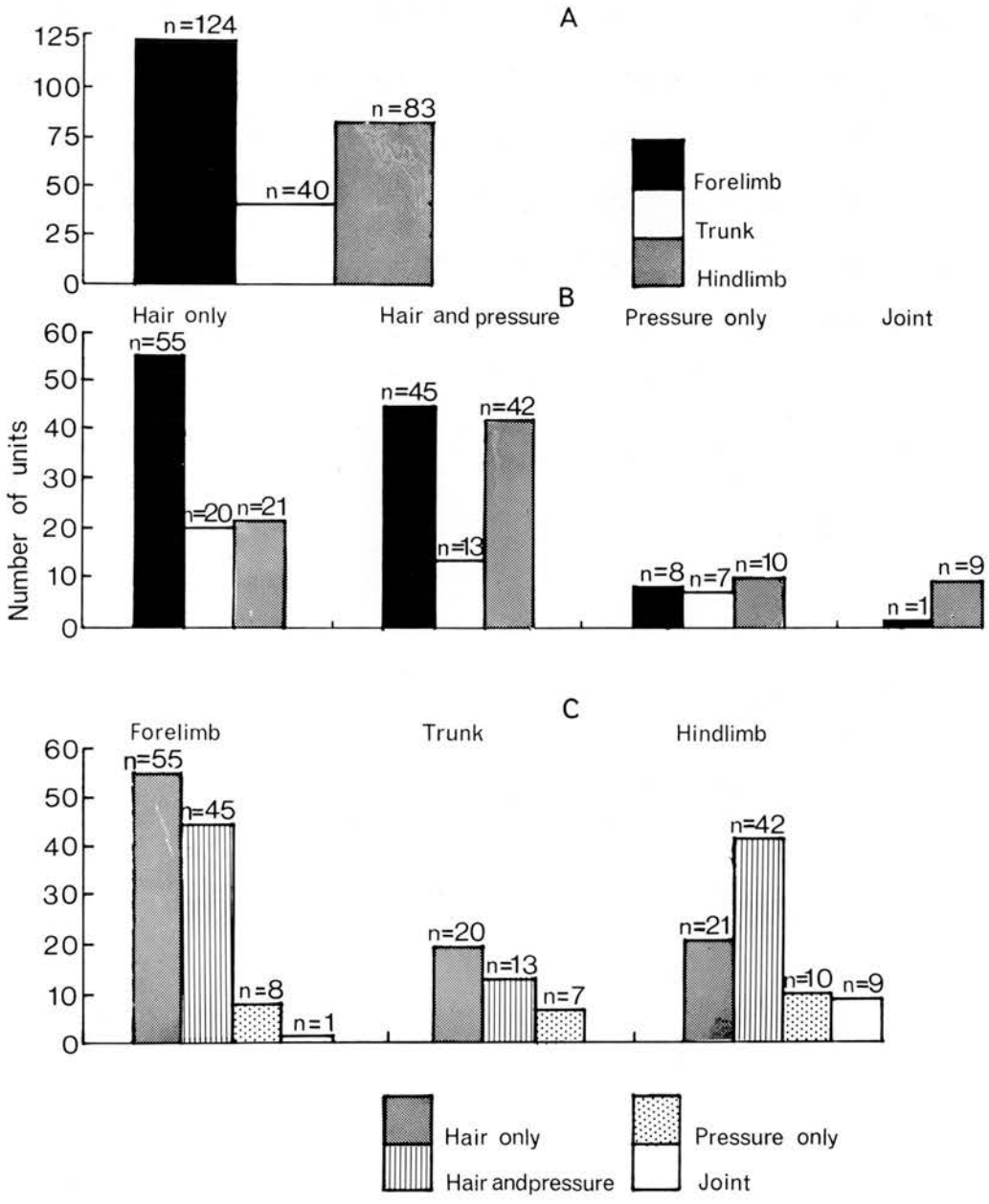

A
125
100
75
50
25
0
n=124
n=40
n=83
Forelimb
Trunk
Hindlimb
B
Hair only
Hair and pressure
Pressure only
Joint
Number of units
60
50
40
30
20
10
0
n=55
n=20
n=21
n=45
n=13
n=42
n=8
n=7
n=10
n=1
n=9
C
Forelimb
Trunk
Hindlimb
60
50
40
30
20
10
0
n=55
n=45
n=8
n=1
n=20
n=13
n=7
n=21
n=42
n=10
n=9
Hair only
Hair andpressure
Pressure only
Joint

Figure 8

Identification of spino-cervical tract units.

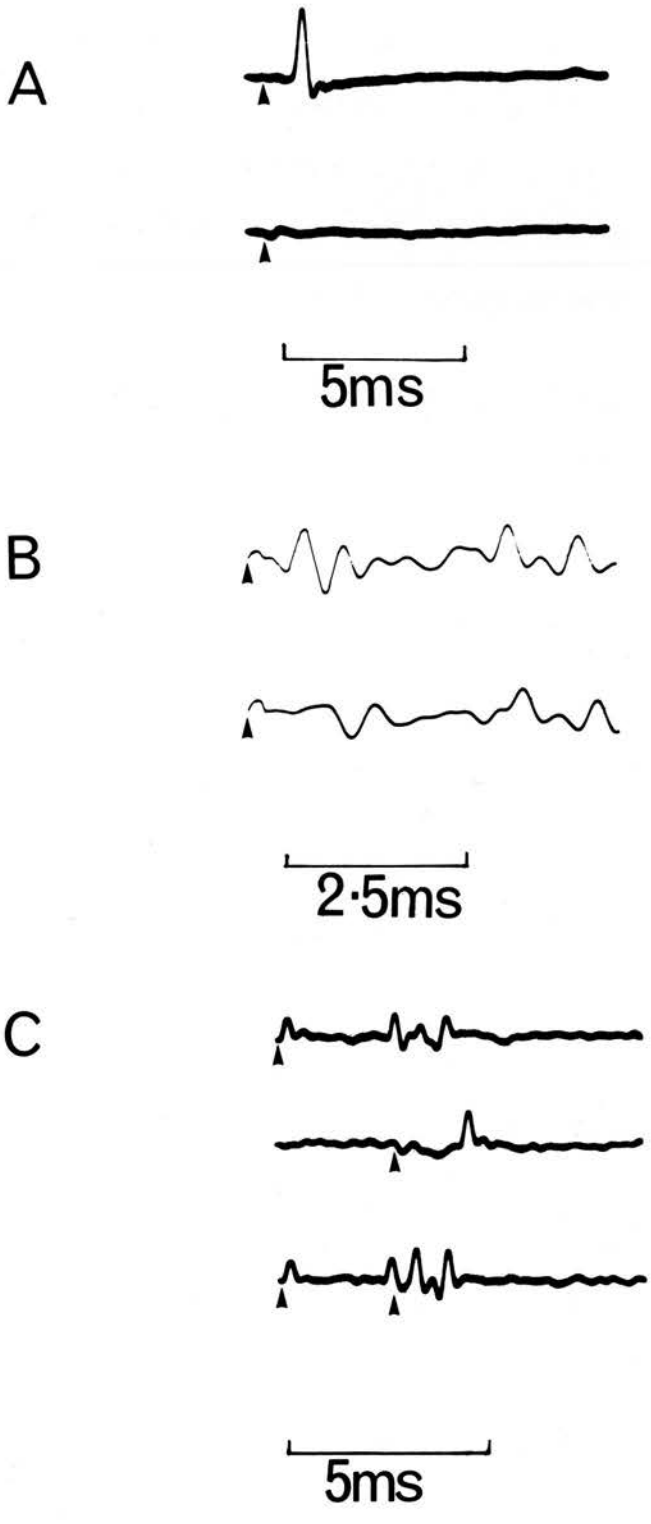
A Top trace: SCT unit being antidromically excited from the C3 stimulating electrode, latency 0.8 ms.
Lower trace: Failure to antidromically excite the same unit from the C1 stimulating electrode. The point of stimulation is marked with an arrow.

B Top trace: Antidromic excitation of an SCT unit from the C3 stimulating electrodes. Latency 0.55 ms.
Lower trace: Antidromic excitation of the same SCT unit from the C1 stimulating electrodes. Latency 1.45 ms.
The conduction distances were C1-C3 = 1.4 cm, C3 - recording electrode = 4.5 cm and hence the corresponding conduction velocities were 40.6 ms^{-1} and 81.8 ms^{-1}. Thus the unit was included in the spinocervical tract. Both traces show later, orthodromic, impulses.

C Collision. The top trace shows orthodromic action potentials evoked in an SCT unit by stimulation of the superficial radial nerve (arrow). The latency of the first orthodromic action potential was 2.7 ms.

The middle trace shows an antidromic action potential evoked by stimulating C3 (arrow) latency 1.6 ms.

The bottom trace shows the result of both stimuli together. There is no antidromic response from C3.


A
5ms
B
2·5ms
C
5ms

fields were divided up into those occurring above and below the elbow and knee joint in the forelimb and hind limb respectively. Units with receptive fields including one of these joints were disregarded. Hind limb units were found to have higher conduction velocities than their forelimb counterparts. The significances of these differences were tested with a small sample Students t test and were found to be not significant (See Table 4 for values of P).

A disadvantage of this analysis is that the differing proportions of the various unit types in the forelimb and hind limb might distort the mean forelimb and hind limb conduction velocities if there were significant differences in the mean conduction velocities between the individual unit types with receptive fields in different locations. Thus the significances of the differences between the mean conduction velocities of the different spino-cervical tract unit types in the forelimb, hind limb and trunk were tested for with a small sample Students t test. This analysis revealed no significant differences in mean conduction velocities. For values of P see Table 5.

Finally it was thought possible that by pooling the experimental results the significance of differences in conduction velocity of the various types of unit in different locations might be lost. This could happen if there was a variation in mean spino-cervical tract axon diameter between different cats. Ekholm (1967) has shown that the diameter of nerve fibres increases after birth. Alternatively the use of different micro-electrodes in

Table 4

Units with receptive fields on the limbs were grouped according to whether their receptive fields were above or below the knee or elbow joint. Receptive fields including one of these joints were disregarded.

Values of P for the significance of the differences between the mean conduction velocities were calculated from a small sample Students t test.

Where $t = \dfrac{\bar{x}}{\sigma\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}}$

σ = standard deviations

n = number of observations

$\bar{x} = \bar{x}_2 - \bar{x}_1$

$\sigma^2 = \dfrac{(n_1-1)\sigma_1^2 + (n_2-1)\sigma_2^2}{n_1+n_2-2}$

	FORE PAW	FORE LEG	HIND PAW	HIND LEG
NUMBER OF UNITS	82	19	58	18
% OF SAMPLE	46.3	10.7	32.8	10.2
MEAN CONDUCTION VELOCITY (ms^{-1})	46.05	40.63	48.18	50.32
STANDARD DEVIATION	19.85	21.76	20.42	19.8

	FORE PAW	FORE LEG	HIND LEG
FORE LEG	$P<0.3$		
HIND PAW	$P<0.5$	$P<0.2$	
HIND LEG	$P<0.5$	$P<0.2$	$P<0.7$

Table 5

The significances of the differences between the mean conduction velocities of the different spinocervical tract unit types in the forelimb, hind limb and trunk were tested for with the small sample Students t test. The table shows maximal values of P.

The unit types are:

H Responding to brushing of hairs only.

H & P Responding to brushing of hairs and the application of a sprung metal clip.

P Responding to pinch or pressure only.

No R.F. No receptive field could be found for these units.

T.B. Responding only to squeezing the base of the tail.

Prefixes F, T and H refer to receptive fields on the forelimb, trunk and hind limb respectively. The units sampled were all those of Table 3.

Mean Conduction Velocity(ms^{-1})	44.8 F.H.	48.6 F.H+P.	40.1 F.P.	37.5 NOR.F	54.1 T.H.	52.1 T.H+P.	41.6 Tail Base	49.6 H.H.	48.1 H.H+P	44.2 H.P.	59.7 H.J.	ms^{-1}
F.H+P.	0.4											
F.P.	0.6	0.3										
NOR.F.	0.3	0.1	0.8									
T.H.	0.2	0.4	0.2	0.1								
T.H+P.	0.3	0.6	0.3	0.2	0.9							
Tail Base	0.8	0.4	0.8	0.6	0.3	0.4						
H.H.	0.4	0.9	0.3	0.1	0.6	0.8	0.4					
H.H+P.	0.5	0.9	0.3	0.1	0.4	0.6	0.5	0.8				
H.P.	1.0	0.6	0.7	0.5	0.4	0.5	0.8	0.4	0.5			
H.J.	0.1	0.2	0.1	0.05	0.6	0.5	0.2	0.3	0.2	0.2		

Table 6

The conduction velocity data of 4 individual experiments, 7328, 7407, 7427 and 7428 are analysed separately and the receptive field locations are shown on figurines.

Values of P were computed with the small sample Students t test.

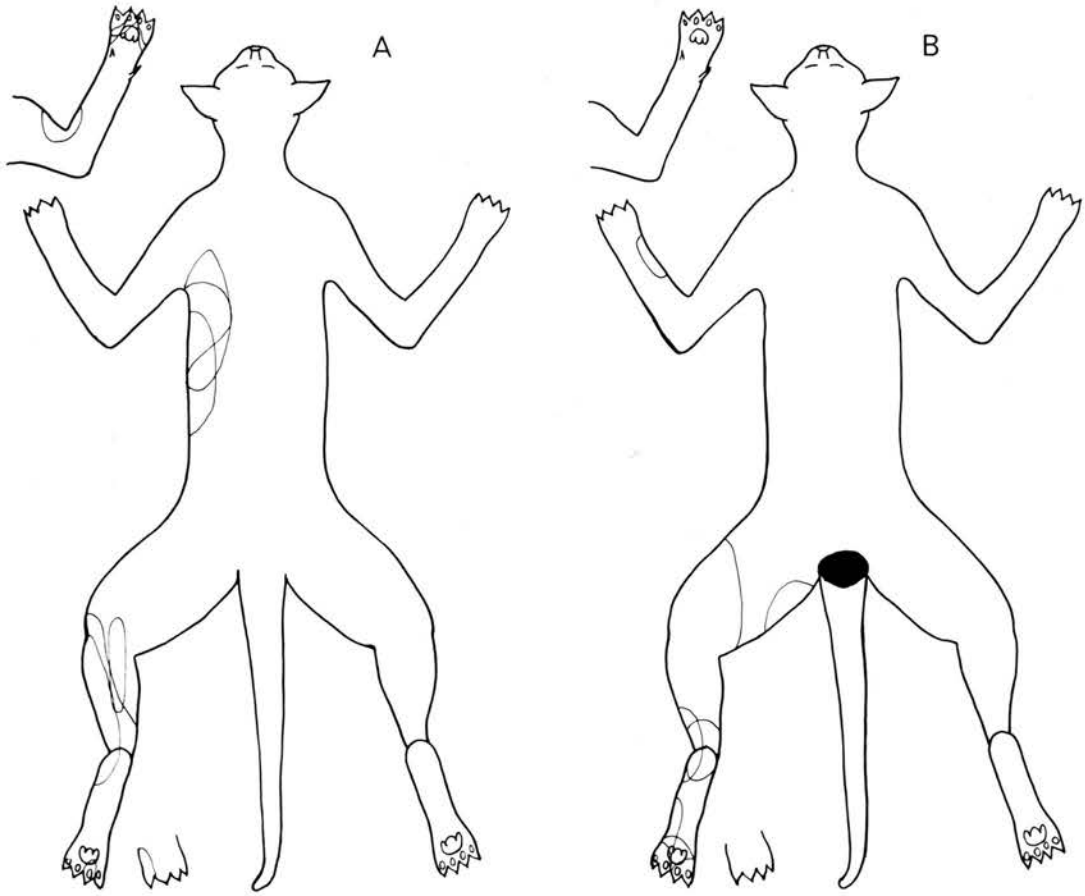
The figurines show:

A 'Hair' receptive fields.

B Hair and pressure receptive fields (clear outlines) and pressure only receptive fields (black).

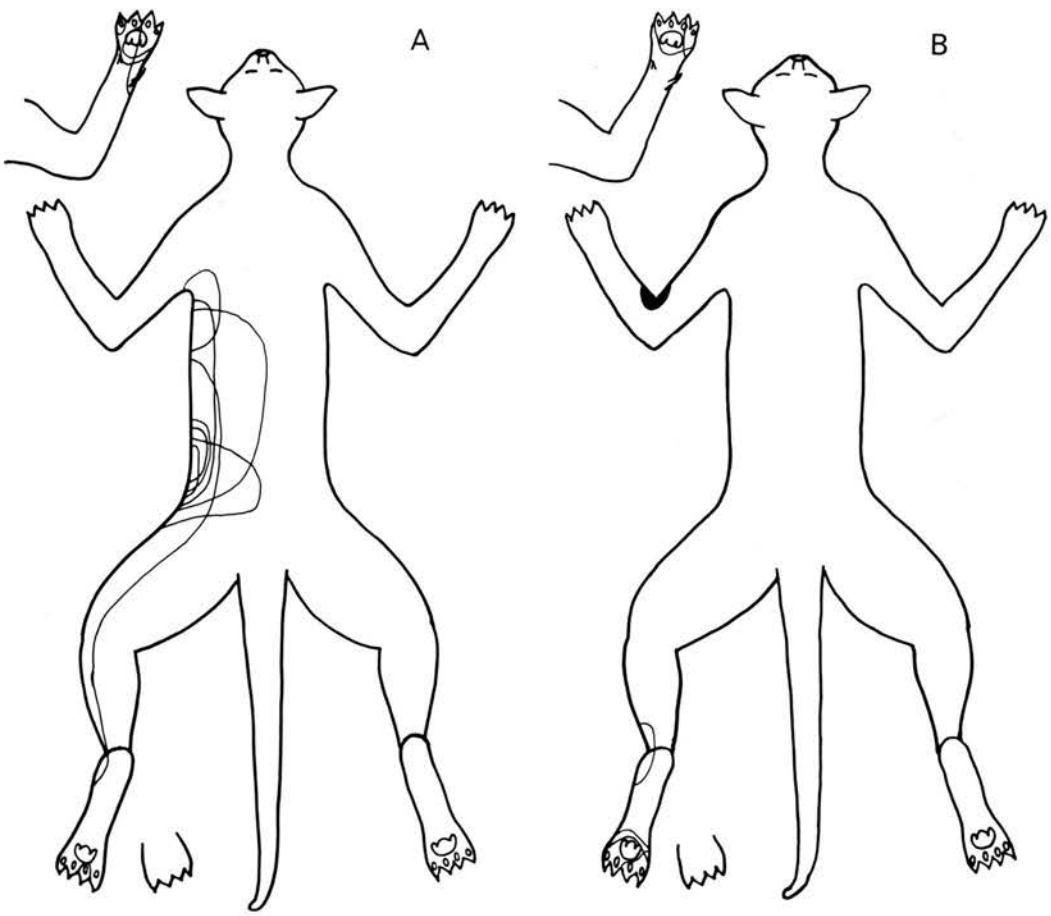
	Forelimb					Trunk				Hind limb				
Exp Total	H	H&P	P	No	J	H	H&P	P	TB	H	H&P	P	No	J
7328 32	6	1	0	3	0	3	2	0	2	5	8	1	0	1
ms^{-1} mean cv. 53.3	28.6	73.0	-	48.2	-	68.0	79.0	-	64.0	67.4	54.7	85.0	-	64.0
st.dev. 21.9	14.7	0	-	30.8	-	19.9	32.5	-	11.3	8.4	21.2	0	-	0
ms^{-1} mean cv.	37.18					70.0				58.9				
st.dev.	22.19					19.2				19.2				

Forelimb vs Hindlimb Hair	$P < 0.001$
Forelimb vs Trunk	$P < 0.01$
Forelimb vs Hindlimb	$P < 0.02$
Trunk vs Hindlimb	$P < 0.2$



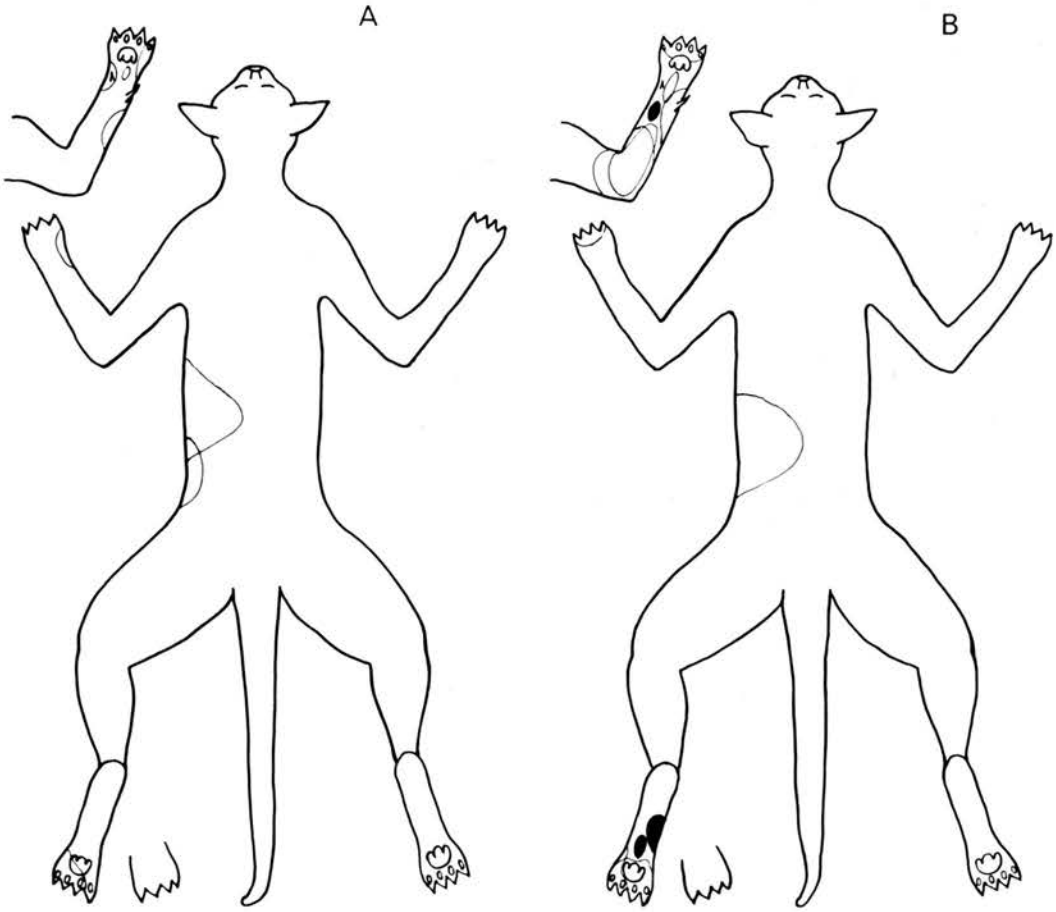
		Forelimb					Trunk				Hind limb				
Exp	Total	H	H&P	P	No	J	H	H&P	P	TB	H	H&P	P	No	J
7407	25	4	2	1	1	0	8	0	0	0	1	4	0	0	4
mean cv.	61.3	48.5	50.0	63	13.2	-	60.0	-	-	-	86.0	77.7	-	-	71.0
ms^{-1} st. dev.	27.47	32.2	18.4	0	0	-	31.1	-	-	-	0	23.1	-	-	16.2
ms^{-1} mean cv.		46.2					60.2				75.6				
st. dev.		26.7					31.1				18.0				

Forelimb vs Trunk	$P < 0.4$
Forelimb vs Hind limb	$P < 0.02$
Trunk vs Hind limb	$P < 0.3$



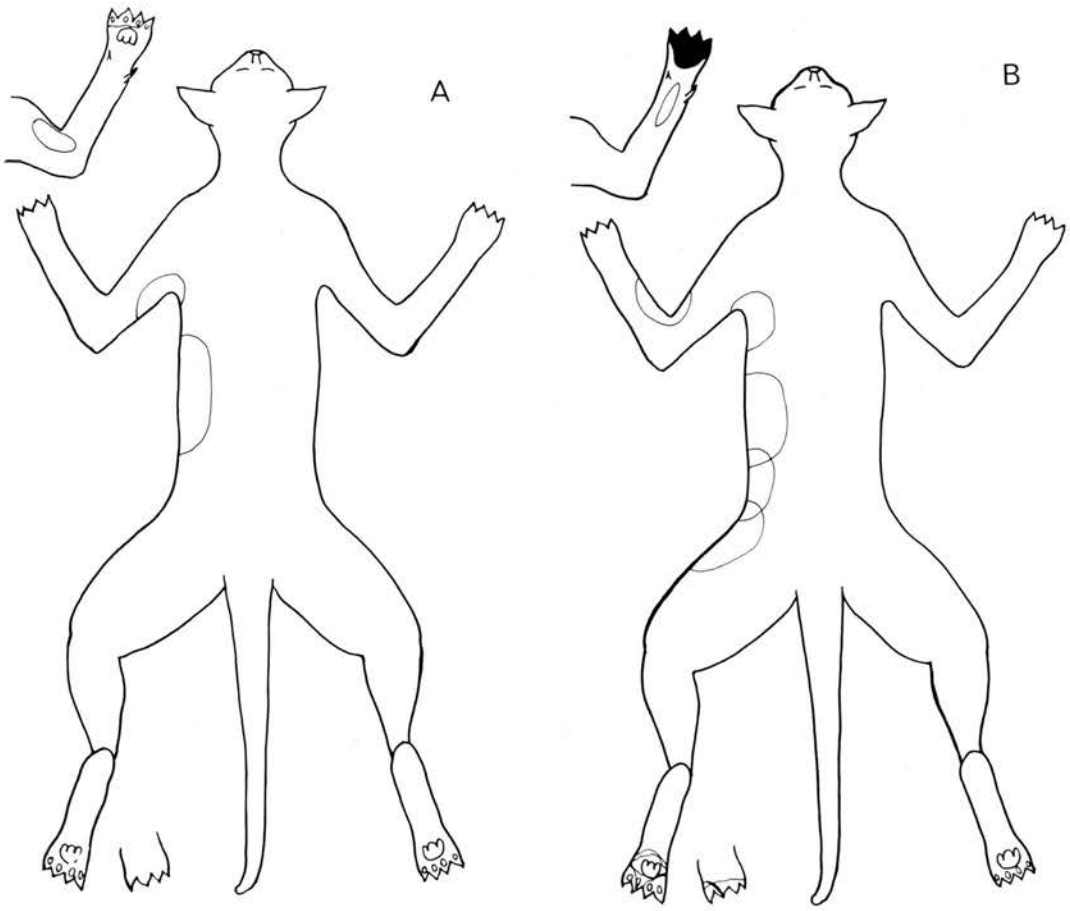
	Forelimb					Trunk				Hind limb				
Exp Total	H	H&P	P	No	J	H	H&P	P	TB	H	H&P	P	No	J
7427 21	5	5	1	2	0	2	1	0	0	1	2	2	0	0
ms^{-1} mean cv. 50.6	59.8	56.0	20	40.0	-	42.5	60	-	-	34	50.5	51.5	-	-
st. dev. 13.8	40.7	10.7	0	14.1	-	12.0	0	-	-	0	0.7	24.7	-	-
ms^{-1} mean cv.	52.2					48.3				47.6				
st. dev.	14.5					12.2				14.5				

Forelimb vs Trunk	$P < 0.7$
Forelimb vs Hind limb	$P < 0.6$
Trunk vs Hind limb	$P < 1.0$



	Forelimb					Trunk				Hind limb				
Exp Total	H	H&P	P	No	J	H	H&P	P	TB	H	H&P	P	No	J
7428 18	3	2	1	1	0	1	3	0	0	0	7	0	0	0
ms-1 mean cv. 38.7	38.5	34.0	60	38	-	38.0	29.3	-	-	-	41.2	-	-	-
st. dev. 12.2	24.1	12.7	0	0	-	0	9.0	-	-	-	6.1	-	-	-
ms-1 mean cv.	40.2					31.5				41.2				
st. dev.	17.3					8.54				6.1				

Forelimb vs Trunk	$P < 0.4$
Forelimb vs Hind limb	$P < 0.8$
Trunk vs Hind limb	$P < 0.05$



different experiments could account for this failure to pick up fine fibres in some experiments.

To test this possibility the results of 4 separate experiments were analysed individually. These were selected simply on the basis of having the greatest number of units. In three of the experiments the mean conduction velocity of hind limb units was greater and in two experiments this difference was moderately significant ($P<0.02$). In the one experiment, where it was possible to compare the conduction velocities of forelimb and hind limb hair units, it was found that the forelimb hair units were considerably slower 28.6 ms^{-1} c.f. 67.4 ms^{-1}. This difference was highly significant $P<0.001$.

The effect of gallamine triethiodide

It was stated in the literature review that gallamine triethiodide excited second order neurones in the dorsal column medial lemniscal system with 'hair' receptive fields. Because of the difficulty in maintaining stability in the cervical cord this substance was used routinely. The duration of its effect, as judged by fasciculation, was from 1-2 hours after which further doses of 20 m g were given by slow intravenous injection. During one experiment it was noticed that the spontaneous discharge of an identified hair only unit increased immediately following the administration of a maintenance dose of 20 m g gallamine triethiodide. The effect was still present five minutes later. This observation was repeated in another hair only

Figure 9

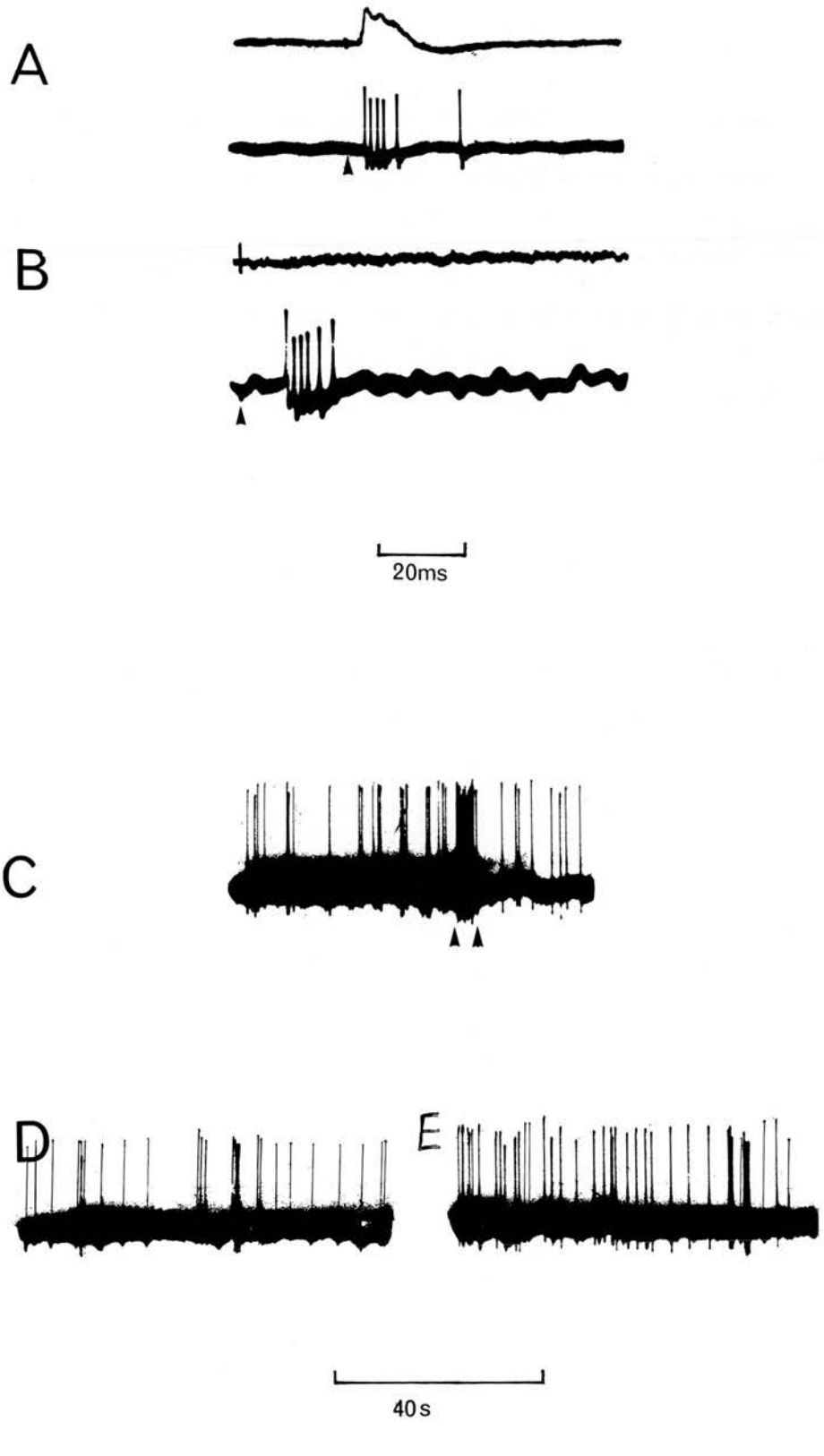
A A SCT unit responding to electrical stimulation of the superficial radial nerve. Latency = 3.5 ms.

B An SCT unit responding to electrical stimulation of the medial plantar nerve. Latency = 10.4 ms.

In each pair the top trace is the cord dorsum potential and the lower trace the micro-electrode recording.

C The spontaneous discharge of a hair and pressure type SCT unit. Arrows mark the application and release of a sprung metal clip.

D and E The spontaneous discharge of a hair only unit, D before and E three minutes after the intravenous injection of 20 mg Gallamine triethiodide.


A
B
20ms
C
D
E
40 s

unit in another cat (Figure 9). Thus it is possible that the use of this paralysant may have biased the sample in favour of hair excited units. This is thought unlikely for two reasons:

(1) the response of the units to natural stimulation of their receptive fields was similar before and after the application of gallamine triethiodide;

(2) Brown and Franz (1969) found no differences in the number of hair excited units in paralysed decerebrate and unparalysed chloralose anaesthetised cats.

Discussion

These results show that there is a physiologically definable forelimb component to the spinocervical tract. The methods of identification were similar to those used by Brown and Franz (1969) who described the hind limb component. Collision of the orthodromically and antidromically evoked action potentials was not used in this section but was used in Section IV where extracellular recordings were made from the cells of origin of the spino-cervical tract. This technique excludes the possibility of transynaptic activation from the C3 stimulating electrode.

Qualitatively the forelimb component is very similar to its hind limb counterpart. Brown and Franz (1969) and Brown (1971) described five types of unit in decerebrate or anaesthetised cats. There were:

Type I: excited by tylotrich hair receptors only.

Type II: excited by movement of guard hairs and sometimes pressure.

Type III: excited by all types of hairs and pressure.

Type IV: excited by pinch or pressure.

Type V: not excited by natural stimulation.

In the present study it was possible to confirm the presence of all these unit types for units with receptive fields in the forelimb. However, because less time was available for typing, most units were placed into four categories which encompassed Brown's typing without the necessity of categorising the type of hair producing the excitation. Thus the "hair only" units of the present study were mostly analogous to Brown's Type I but may also have included Type II units with no pressure component. Similarly the "hair and pressure" units were analogous to Brown's Type III but may also have included Type II units with a pressure component. Types IV and V of Brown correspond with the "pressure only" and "no receptive field" units described in this section.

The "joint movement" units have not been previously described as belonging to the spino-cervical tract. However there is evidence that high threshold muscle and joint afferents may excite the spino-cervical tract (Lundberg and Oscarsson, 1961; Hongo, Jankowska and Lundberg, 1968) but this evidence was from electrical stimulation of nerves rather than natural stimulation of the joint itself. It would be of interest to know if joints other than the metatarsal phalangeal and metacarpal phalangeal joints

influenced spino-cervical tract activity and if they also did so with a preferential direction of movement. However this was outside the scope of the experiment's design.

A possible criticism of these results would be that the test for pressure was a sprung metal clip. This would be expected to excite low threshold pressure receptors such as the slowly adapting types I and II (Chambers and Iggo, 1967) and probably also the nociceptor afferents with fibres in the $A\delta$ and C conduction velocity ranges. Thus no attempt was made to decide the difficult but physiologically important question of which units were potentially nociceptive. Certainly most of the pressure only units responded more vigorously to pinch than to the clip.

More units in this study were of the pinch and pressure type (7.2%) than seen by Brown and Franz (1969) in decerebrate or anaesthetised cats (0.6%). A possible explanation for this lies in the different preparations used. Brown and Franz cut the dorsal columns caudal to C3. This procedure could not be employed efficiently in the present experiments as (1) the recording site was between C4 and C5 and such a section might have damaged axons through ischaemia and changes in the ionic content of the extracellular fluid. (2) it would have been necessary to cut the fasciculus cuneatus to prevent orthodromic excitation of forelimb spino-cervical tract cells by antidromic excitation of dorsal column collaterals at the C3 stimulating site. A consequence of this difference in the preparations is that there may have been a greater degree of tonic

descending inhibition acting on the units described in this section as the dorsal columns are known to activate and convey descending systems which inhibit the spino-cervical system (Brown and Martin, 1973; Brown, Kirk and Martin, 1973). Thus the greater number of "pressure only" units may be due to the inhibition of units which would exhibit more sensitive receptive fields if the dorsal columns were cut. A similar argument would explain why Brown and Franz (1969) observed a spontaneous discharge in all but one of their units whilst this was only observed in 17% of units in the present study. Wall (1967) showed that spontaneous discharges in dorsal horn cells was dependent on the activity of primary afferent fibres.

No evidence could be found for a projection of slowly adapting type I receptors, carpal hair afferents or pad or claw receptors to the spino-cervical system. The role of the carpal hair afferents remains an enigma as nothing has yet been reported about their central connections.

A discussion of the relative numbers of different spino-cervical unit types in different locations requires the assumption that the tract was randomly sampled. The conduction velocity histogram shows that fibres of $2\mu M$ to $18\mu M$ were encountered when Hursh's(1939) conversion factor is used. The mean conduction velocity was 12.1 ms^{-1} slower than that reported by Brown and Franz (1969) but 3.4 ms^{-1} faster than that found by Bryan, Trevino, Coulter and Willis (1973) who recorded from cell bodies. However a

comparison with studies made in the lumbo-sacral spinal cord may not be justified as it is not known if spino-cervical tract axons taper as they approach the lateral cervical nucleus.

The predominance of forelimb units in the sample is not surprising as Horrobin (1966) found 94 units in the lateralcervical nucleus with receptive fields in the forelimb and rostral trunk but only 39 units with more caudal receptive fields. Brown, Gordon and Kay (1973) in a study of axons in the medial lemniscus found that 88% of units had receptive fields on the forelimb or upper trunk. As most of their units were considered to be part of the dorsal column - medial lemniscal system it seems likely that in both systems there is preferential access to higher centres for units with forelimb receptive fields. This may reflect the greater importance of the forelimb in tactile exploration.

Also striking is the difference in the percentage of forelimb units in the spino-cervical system compared with the dorsal column system as found by Brown, Gordon and Kay (1973). It would seem that the dorsal column system is even more concerned with forelimb information than the spino-cervical system.

It appears that in the spino-cervical system it is those forelimb units which would be most useful in exploration of the environment that are favoured most. Not only is there a significant difference in the proportion of hair only units to other units between

forelimb and hind limb in the spino-cervical tract but these forelimb hair only units also appear to get more direct access to higher centres when they are processed in the Lateral Cervical Nucleus. Horrobin (1966) found 112 hair only units but only 12 light pressure units in the nucleus.

Horrobin (1966) found that within the lateral cervical nucleus relay cells with forelimb receptive fields had a tendency to be located more laterally than their hind limb counterparts. In the present study no evidence could be found for a topographical organisation of axons in the spino-cervical tract.

The analysis of conduction velocity of the various unit types in different locations yielded disappointing results. It was hoped that it might be shown that units with proximal receptive fields are preferentially slowed to allow the brain to process coinciding events simultaneously. There is some evidence that corticofugal inhibition of the dorsal column nuclei follows this pattern (Cole and Gordon, 1976). In two of the individually analysed experiments there was a significant difference in conduction velocity between forelimb and hind limb units and the difference between forelimb and hind limb hair only units was particularly interesting as Brown (unpublished data) has noticed a similar difference between type I hair only units with receptive fields on the hind limb and trunk.

Unfortunately the bulk of the conduction velocity analysis results are insignificant statistically and it

is unreasonable to put too much emphasis on the individual experiments. It would be of interest to know if the conduction velocities of axons measured in the cervical cord reflects their conduction velocities in the thoracic and lumbar cord.

In conclusion these results demonstrate that there is a forelimb component to the spino-cervical tract which is qualitatively similar but quantitatively more important than the hind limb component.

Section III

Homo-segmental and Hetero-Segmental Inhibition of Transmission through the Spinocervical tract in Decerebrate Cats

INTRODUCTION

The experiments in this section were performed to elucidate the nature and extent of the inhibitory influences, from segmental sources, on spino-cervical tract units present in the cervical spinal cord. It is known that units with receptive fields in the hind limb may be inhibited from receptors on the trunk, ipsilateral or contralateral hind limb (Brown, 1968b) and that tetanisation of the contralateral superficial radial nerve inhibits hind limb units (Taub, 1964). It is not known if spino-cervical tract units with receptive fields in the forelimb are subject to segmental inhibition or if units with receptive fields in the hind limb may be inhibited by cutaneous stimulation of the forelimb.

METHODS

The experiments were those of Section II with the addition of two cats prepared in a similar manner but in which spino-cervical tract somata were recorded from as is described in section IV. After these two cats had been investigated in the decerebrate state they were spinalised at the Atlanto-occipital joint with a blunt spatula. Bleeding from this wound was diminished with the gelatine foam 'Steripson'. Changes in the cat's blood pressure occurred and were noted after spinalisation.

Those units which could be excited from one of the exposed peripheral nerves were investigated for segmental inhibition by means of electrical stimulation of the remaining peripheral nerves at varied conditioning intervals. To do this the stimulus or 'test' shock was a single 0.2 ms pulse of a voltage just sufficient to elicit a train containing a constant number of impulses against which inhibition could be looked for. This stimulus voltage was 1.7 -7.2 times greater than the threshold of voltage for the 18 units excited by electrical stimulation of the peripheral nerves. The conditioning shock was either a single 0.2 ms pulse or more commonly a train of 3 or 4 0.2 ms 500 Hz. pulses. The voltage of the conditioning stimulus was 2-10 times greater than the threshold voltage.

Time courses of segmental inhibition were plotted by expressing the number of impulses in five conditioned impulse trains as a percentage of the number in five unconditioned trains. The interval between the testing

stimulus /

and the first of the conditioning stimuli was varied between 10 and 150 m.s.

Natural stimulation was also used as an inhibitory stimulus for 9 units with a spontaneous discharge and in the other 19 units when a discharge was evoked by applying a clip to its excitatory receptive field or by brushing the hairs of its excitatory field. Pinch or pressure or brushing hairs with an artist's brush were used as inhibitory stimuli. When found, the extent of the inhibitory as well as the excitatory receptive fields were mapped as figurines.

Results

The results of this section were drawn from 7 cats used in section II (22 units) and 2 cats from which only forelimb spino-cervical tract cells were sampled (6 units). Because inhibitory receptive fields were looked for against a discharge usually evoked by application of a metal clip there is a bias in favour of units whose receptive field contained a pressure component. (Figure 10)

All the units in this section are drawn from cats which showed evidence of segmental inhibition. Experiments in which inhibition was absent were discarded; lack of segmental inhibition was considered to be due to a poor physiological state. Units were selected for inclusion on the basis of having had the cat's surface area thoroughly searched for inhibitory receptive fields.

Figure 10

The conduction velocity histogram of the units of Section III.

A Whole sample Mean 45.9 ms^{-1}

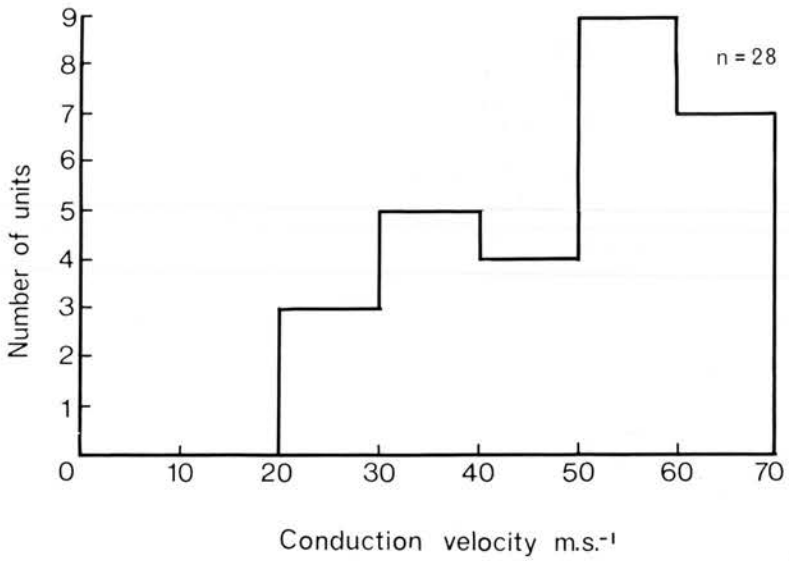
Range 20-65 ms^{-1}

Standard deviation 13.1

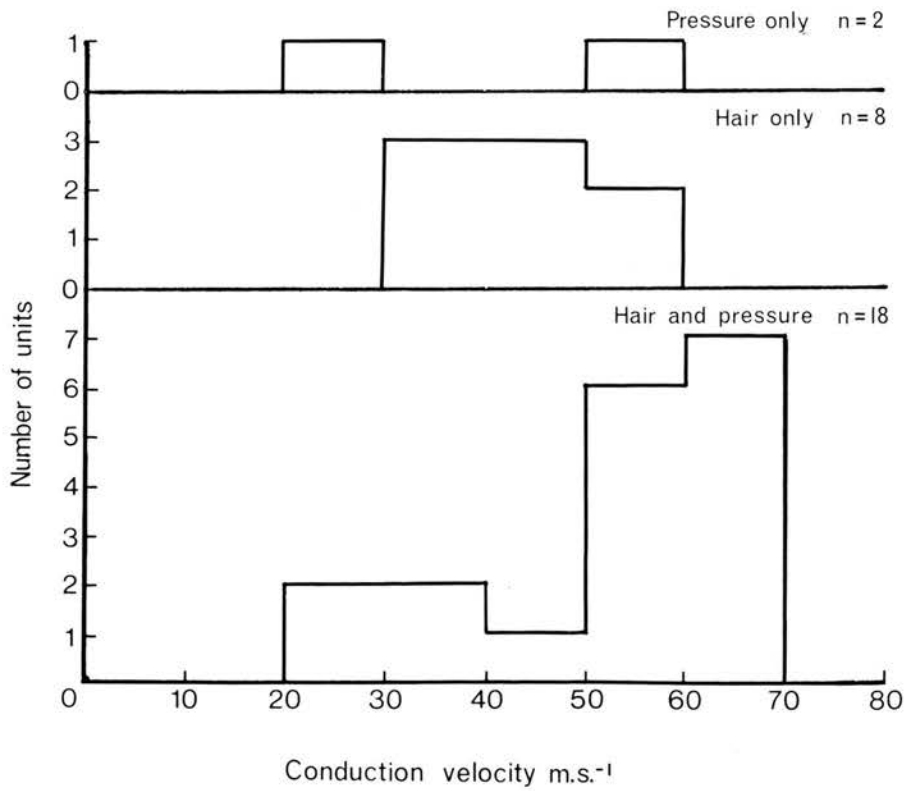
B The sample subdivided into unit types

	Hair only	Hair & Pressure	Pressure onl
Mean	42.1	49.4	30 ms^{-1}
Range	30-54	20-65	20-40 ms
Standard deviation	7.7	13.7	14.1

A


n = 28
Number of units
0
1
2
3
4
5
6
7
8
9
10
20
30
40
50
60
70
Conduction velocity m.s.-1

B


Pressure only n = 2
Hair only n = 8
Hair and pressure n = 18
Number of units
0
1
2
3
4
5
6
7
10
20
30
40
50
60
70
80
Conduction velocity m.s.-1

Inhibition elicited by electrical conditioning of peripheral nerves

For a given stimulus voltage, trains of conditioning impulses were found to be more effective than a single conditioning shock. Inhibition could be elicited from all of the other three exposed peripheral nerves in 8 out of 10 units tested and in the contralateral homologous nerve in all of the 18 units which could be excited by electrical stimulation of an exposed nerve.

At its maximum, inhibition was of greatest amplitude and was least delayed from the contralateral homologous limb and of least amplitude from the heterologous contralateral limb. The P wave of the cord dorsum potential recorded in the spinal segment C5-C6 was similarly most easily elicited from the forelimb and least easily if at all from the contralateral hind limb.

P waves elicited by stimulation of the contralateral superficial radial nerve occurred with stimulus intensities of 0.9 -3.1 volts. Stimulation of the medial plantar nerve with a 10 volt shock which was the maximum available often failed to evoke P waves.

It was noted that segmental inhibition was most effective against the later discharges in an evoked train of impulses. The first impulse in a train was never seen to be inhibited. (Figures 11 and 12)

Homosegmental inhibition from the contralateral superficial radial and medial plantar nerves was maximal at a conditioning - testing interval 30 - 40 m s, the interval

Figure 11

The inhibition of an SCT cell with a forelimb receptive field by 3, 0.2 ms 500 Hz pulses of 7.0 x threshold for the unit applied to the ipsilateral medial plantar nerve.

A and B show the control response to stimulation of the superficial radial nerve and the associated cord dorsum potential. The conditioning-testing intervals in the other traces are:

C 15 ms

D 20 ms

E 35 ms

F 50 ms

G 80 ms

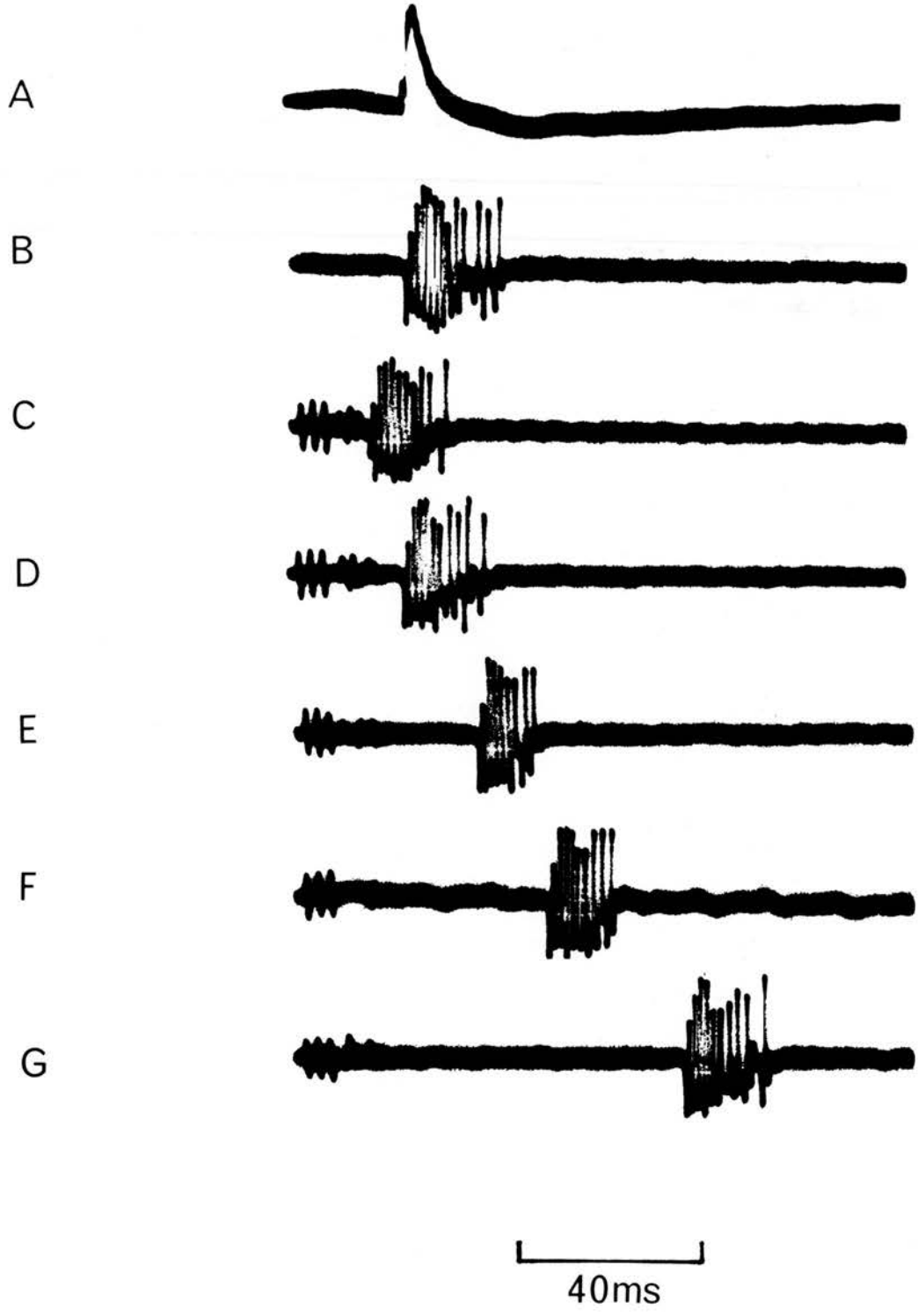

A
B
C
D
E
F
G
40ms

Figure 12

A The spontaneous discharge of a hind limb SCT unit being inhibited by tetanisation of the contralateral medial plantar nerve (arrow) with 0.2 ms 300 Hz 0.5 v pulses.

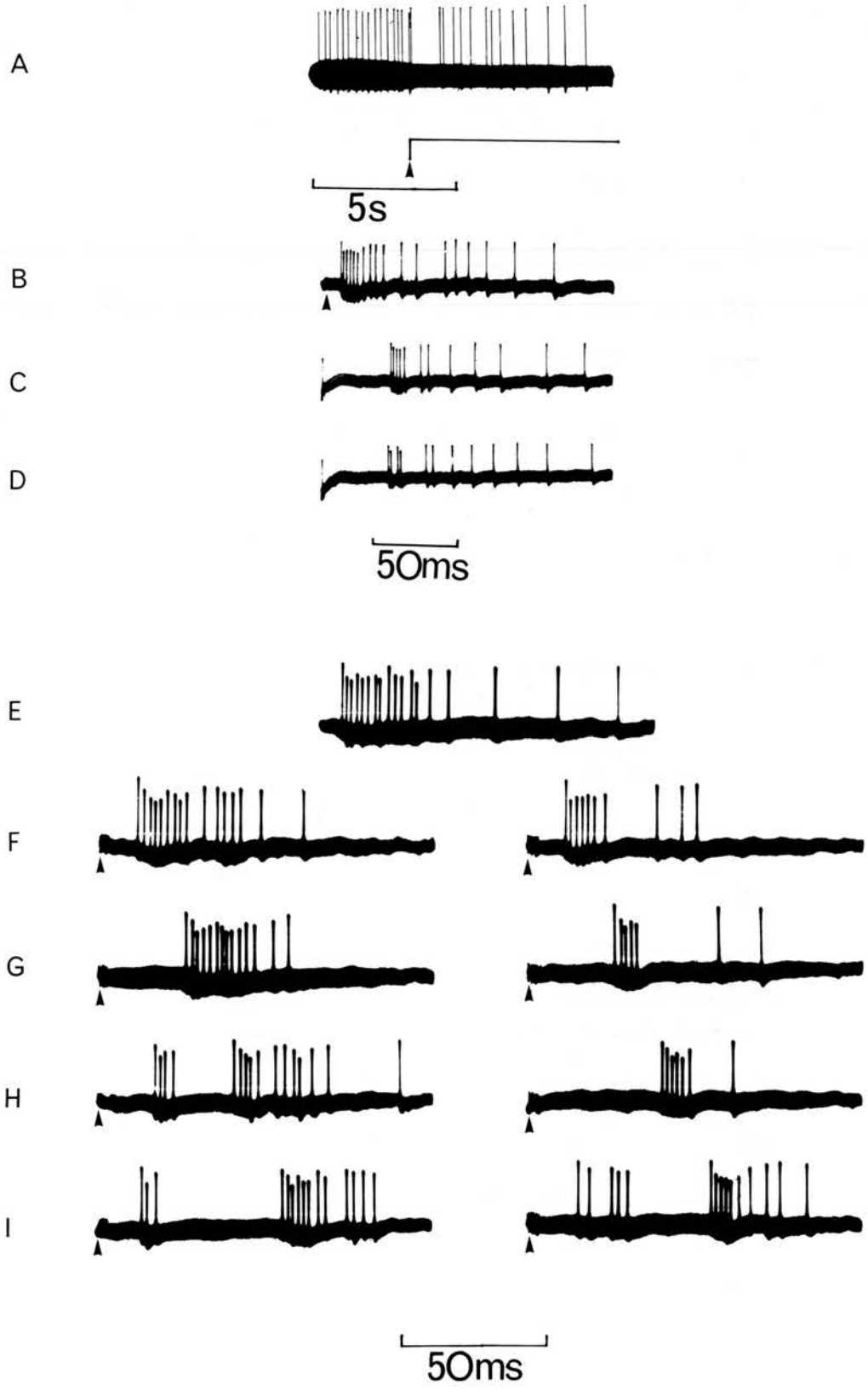
B The unconditioned response of an SCT unit to stimulation of the medial plantar nerve (arrow). The test stimulus was 2.5 times threshold.

C A conditioning pulse of 8.0 times threshold applied to the contralateral superficial radial nerve conditioning testing interval 33 ms.

D A conditioning pulse of 8.0 times threshold applied to the ipsilateral superficial radial nerve. Conditioning testing interval 33 ms.

E A control response of a hind limb SCT unit to stimulation of the medial plantar nerve (arrow) with a 0.2ms 3.5 x threshold pulse.

F, G, H and I the response conditioned by 3, 500 Hz, 0.2ms pulses in the ipsilateral superficial radial nerve (3.0 x T) (Right) and the contralateral medial plantar nerve (3.0 x T) (Left). The conditioning-testing intervals are 5, 25, 40 and 58 ms. Spontaneous action potentials are seen before the test stimulus in H and I


A
5s
B
C
D
50ms
E
F
G
H
I
50ms

being timed from the beginning of the conditioning train. Inhibition was still present at testing intervals of 150 m s. Inhibition elicited from the medial plantar nerves on units with forelimb receptive fields and inhibition elicited from the superficial radial nerves on units with hindlimb receptive fields (heterosegmental inhibition) was maximal at conditioning - testing intervals of 40 -50 m s and was of lesser intensity and was not so prolonged when conditioning pulses of the same voltage were applied to both homosegmental and heterosegmental nerves (Figure13).

For homosegmental inhibition of units with forelimb receptive fields the time course of the 'P wave paralleled the time course of the inhibition.

Decerebrate cats made spinal

Two decerebrate cats which had each previously yielded three spino-cervical tract units receiving inhibition from all the remaining exposed peripheral nerves were made spinal at the level of the Atlanto-occipital junction. This operation was accompanied by a brief increase in blood pressure followed by a sustained fall. In each experiment an attempt was made to continue recording from a unit during spinalisation: on both occasions this was unsuccessful. In one cat the mean blood pressure fell from 75mmHg to 50 mmHg and in the other from 110mmHg to 65 mmHg. In both cats two S.C.T. units were subsequently sampled which were inhibited by conditioning the contralateral superficial radial nerve but not the hind limb nerves. In the cat with the 65mmHg.

Figure 13

The time course of homosegmental and heterosegmental inhibition in decerebrate cats. The conditioning-test interval was the time between the beginning of the conditioning stimulus and the beginning of the test stimulus. Each point represents the ratio of the number of impulses in 5 conditioned and 5 unconditioned impulse trains. All shocks were 0.2ms square waves.

Abbreviations:

I = ipsilateral
X = contralateral
MPN = medial plantar nerve
SRN = superficial radial nerve
T = electrical threshold of unit

Homosegmental inhibition

A

■---■ A single shock of 3.0 x T to the XMPN was used to condition a discharge evoked by a 2.7 x T shock to the IMPN.

▲—▲ A single shock of 3.5 x t to the XSRN was used to condition a discharge evoked by a single 3.0 x T shock to the ISRN.

●—● 3, 500 Hx. shocks of 5.0 x T to the XSRN were used to condition a discharge evoked by a single shock of 2.8 x T to the ISRN.

Heterosegmental inhibition

B

Both plots are of the same Hair and Pressure type unit.

▲—▲ A single shock of 6.0 x T to the ISRN was used to condition a discharge evoked by a single 3.0 x T shock to the IMPN.

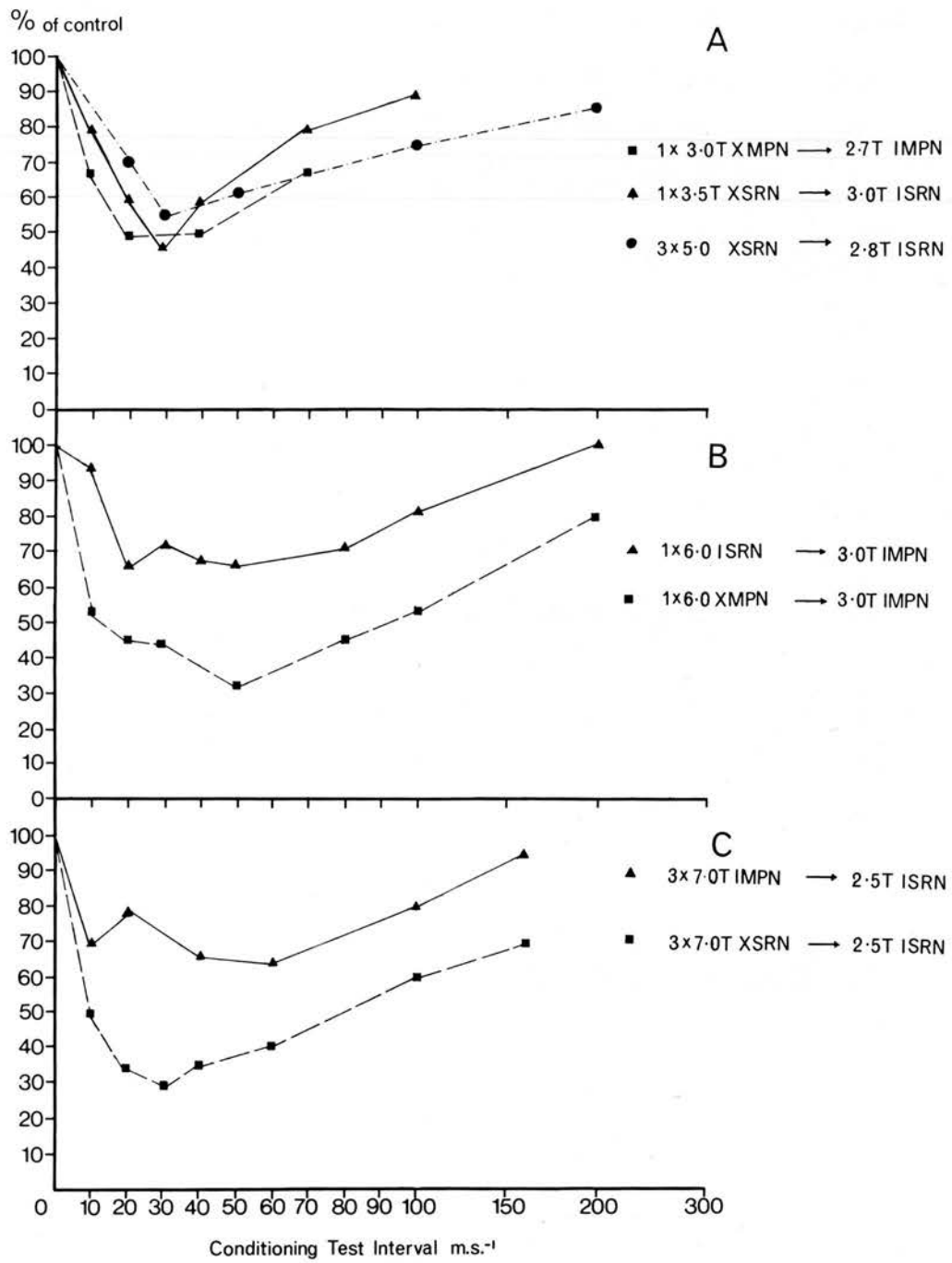
■---■ A single shock of 6.0 x T to the XMPN was used to condition a discharge evoked by a single 3.0 x T shock to the IMPN.

C

Both plots are of the same Hair only unit.

▲—▲ 3, 500 Hz. 7.0 x T shocks to the IMPN were used to condition a discharge evoked by a 2.5 x T shock to the ISRN.

■—■ 3, 500 Hz. 7.0 x T shocks to the XSRN were used to condition a discharge evoked by a 2.5 x T shock to the ISRN.


% of control
A
1× 3·0T XMPN → 2·7T IMPN
1×3·5T XSRN → 3·0T ISRN
3×5·0 XSRN → 2·8T ISRN
B
1×6·0 ISRN → 3·0T IMPN
1×6·0 XMPN → 3·0T IMPN
C
3×7·0T IMPN → 2·5T ISRN
3×7·0T XSRN → 2·5T ISRN
0 10 20 30 40 50 60 70 80 90 100 150 200 300
Conditioning Test Interval m.s.-1

blood pressure the inhibition from the contralateral superficial radial nerve appeared greater than that seen before spinalisation.

Natural stimulation of inhibitory receptive fields

The most effective form of natural inhibitory stimulation was pinch or pressure applied to the ankle, toes or base of the tail. Brushing of hairs was only an inhibitory stimulus for three of the units examined. In these units large areas of skin were involved. In two instances these were on the trunk and once on the contralateral limb.

Of the 28 units for which the body surface was examined, 23 units were found to have inhibitory receptive fields. No relationship between inhibitory and excitatory receptive field locations or types was evident although the three units inhibited by hair only stimulation all had excitatory receptive fields on the forelimb of the hair and pressure type. More than one inhibitory receptive field was sometimes present for a given unit. There was a tendency for inhibitory fields to be on either the contralateral homologous limb or on the other ipsilateral limb. The pads were common sites for inhibitory receptive fields (Figure 14).

Of the 5 units for which no inhibitory receptive field could be found 2 could be excited from the superficial radial nerve and these units were inhibited by conditioning trains in the contralateral superficial radial nerve.

Figure 14

The excitatory (black) and inhibitory receptive fields of the 28 units.

A Excitatory receptive fields of the Hair and pressure type

B Excitatory receptive fields of the Hair only type.

C Excitatory receptive fields of the Pressure only type.

"Pressure and Pinch" inhibitory receptive fields are shown in white.

"Hair" inhibitory receptive fields are shaded.

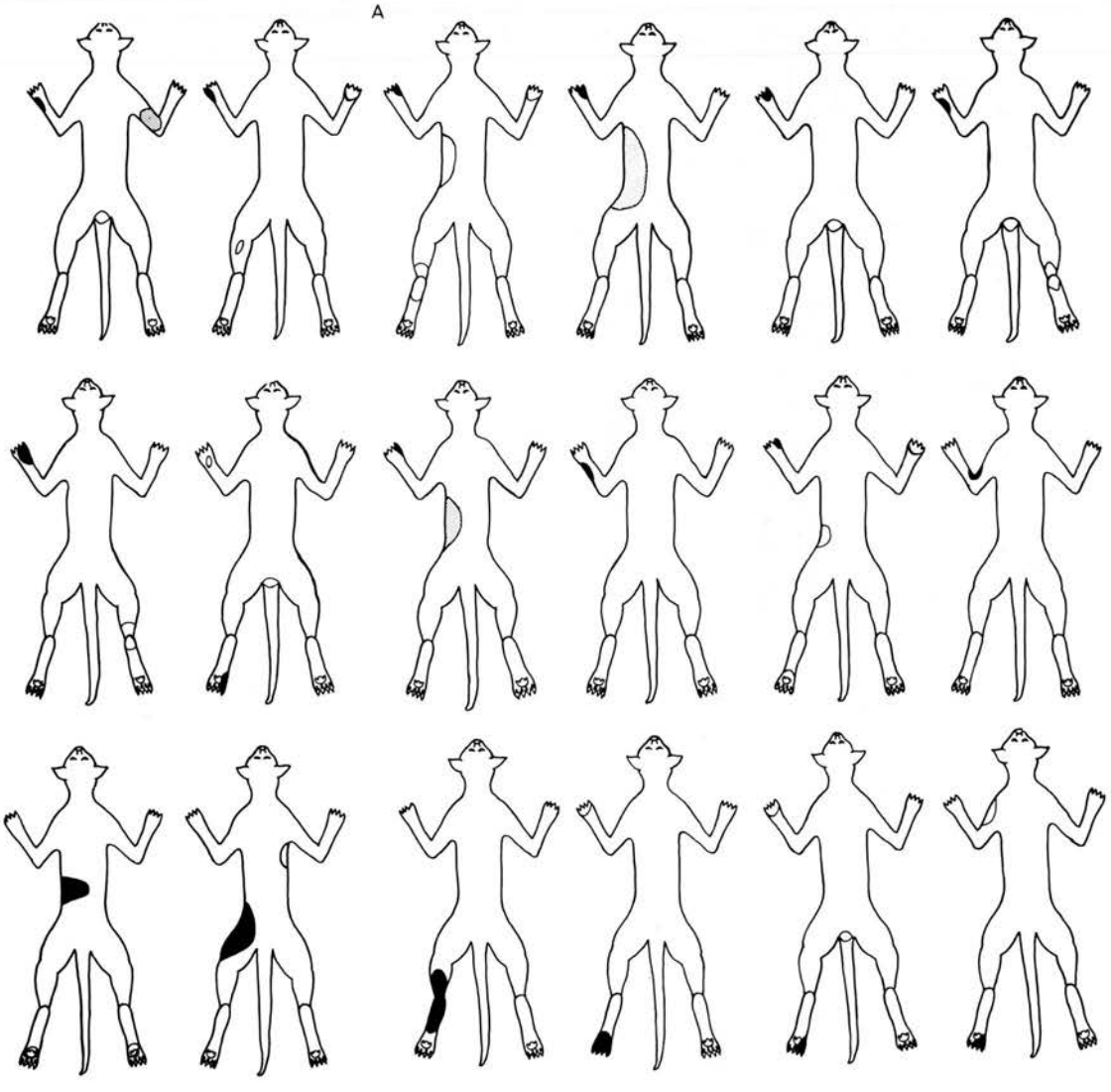

A

Table 7

This summarises some of the data of Section III. The 28 units are arranged chronologically downwards. The first 4 digits of the unit number is the experiment's number.

Receptive field types were identified as:

H Responding to brushing of hairs only.

H & P Responding to brushing of hairs and the application of a sprung metal clip.

P Responding to pressure only.

H,P Denotes separate inhibitory receptive fields of the H or P type.

Postscripts f, t, h signify excitatory receptive field locations.

The finding of inhibition from one of the peripheral nerves is denoted by +. No inhibition is denoted by -. The superficial radial nerve (SRN) and medial plantar nerve (MPN) are prefixed by I or X depending on whether they were ipsi- or contra- lateral to the recoding electrode.

The 9 units with a spontaneous discharge were all inhibited by natural stimulation of their inhibitory receptive fields.

Unit Number	Receptive Field type		Electrically evoked discharges inhibited by electrical stimulation of				Inhibition of spontaneous discharge by natural stimulation	Conduction Velocity of Axon ($m.s.^{-1}$)
	Excitatory	Inhibitory	ISRN	XSRN	IMPN	XMPN		
7411 04	H&P t	P	+	+		+	+	57
10	H h	P					+	41
13	H&P h	None						50
14	H&P f	P		+			+	65
7413 14	H&P h	P						44
7425 09	H&P f	H,P		+				21
10	H&P f	P		+			+	50
7426 01	P h	None						40
05	H f	None		+				39
11	H f	P		+			+	54
7427 05	H&P f	P						50
12	P f	P		+				20
20	H&P h	P	+	−		+		61
22	H&P t	P						60
7428 01	H&P h	P	+	+		+		50
02	H f	P					+	43
12	H t	P					+	38
14	H&P h	P	−	−		+		34
20	H&P f	None						20
7429 02	H&P f	P		+				60
07	H&P f	H,P						60
11	H&P f	H,P		+				30
7647 01	H&P f	P		+	+	+	+	54
02	H&P f	None		+	+	+		40
03	H f	P		+	+	+		60
7648 01	H&P f	P		+	+	+	+	60
02	H f	P		+	+	+		52
03	H f	P		+	+	+		30

Discussion

These results show that the forelimb component of the spino-cervical tract is subject to a similar form of segmental inhibition to that found on hindlimb units and that units with their receptive field in one limb may be inhibited by natural stimuli to any of the other limbs but most commonly to the contralateral homologous or the other ipsilateral limb. (Table 7)

The nature and extent of the inhibitory receptive fields are similar to those described by Brown (1968b) on the hindlimb and caudal trunk. The significance of inhibition elicited by pinching the base of the tail is unclear although this phenomenon was also seen by Brown (1968b). In general the more distally situated inhibitory receptive fields required stronger forms of natural stimulation such as pinching.

Electrical stimulation of the contralateral homologous nerve was the most effective inhibitory stimulus and caused inhibition of discharges even when no inhibitory receptive field could be found. As the superficial radial nerve is purely cutaneous in derivation lack of inhibitory receptive fields on the forelimb might be due to damage of the nerve distal to the stimulating electrode or to the artificial nature of synchronous trains of impulses.

No attempt was made to test for the effects of muscle afferents on spino-cervical tract cell discharges although Hongo, Jankowska and Lundberg (1968) reported an inhibitory action. The medial plantar nerve contains muscle afferents

and it is possible that these are responsible for some of the inhibition elicited by stimulating this nerve.

The time course of the segmental inhibition of forelimb spino-cervical tract units elicited by conditioning impulses from the contralateral forelimb is similar to that described by Brown, Kirk and Martin (1972) and is suggestive of a presynaptic mechanism. The observation that the last impulses in each train are most sensitive to inhibition again supports their suggestion that it is the polysynaptically evoked impulses that are being eliminated.

The observation of limb-limb interactions in the spino-cervical tract has previously been made by Taub (1964). However he did not state whether this phenomenon occurred in spinal or decerebrate cats. Limb-limb inhibition could be conveyed either by direct long ascending or descending spinal pathways such as have been demonstrated for the motor reflexes (Rustioni, Kuypers and Holstege, 1971) or by ascending fibres activating descending inhibitory tracts originating rostral to the spinal cord. Alternatively it is possible that ascending interactions are an intrinsic property of the spino-cervical tract and are mediated by axon collaterals of spino-cervical tract units.

Any experiment involving irreversible spinalisation is open to the interpretation that the changes observed after spinalisation were a consequence of trauma rather than interruption of the ascending and descending fibres. However the fact that segmental inhibition was still

present on stimulation of the contralateral forelimb would support the hypothesis that hind limb inhibition of forelimb units is mediated by pathways involving neurones rostral to the spinal cord. The latencies and time courses of the limb-limb interactions are compatible with either hypothesis.

The pathways by which forelimb stimulation inhibits hind limb spino-cervical tract cells were not investigated. This problem can probably be most easily tackled by recording from the lumbosacral cord and selectively sectioning the thoracic spinal cord. It is known (Wall, 1967) that cooling the spinal cord below the sympathetic outflow can block descending fibres without the concomittant drastic falls in blood pressure found when the cervical cord is cooled.

Section IV

Ipsi- and Contralateral Corticofugal Inhibition of Transmission through the Spinocervical Tract

INTRODUCTION

The experiments in this section were designed to answer the question of whether the forelimb component of the spino-cervical tract is subject to cortico-fugal inhibition and, if so, which areas of the somatosensory cortex are responsible for producing this inhibition?

It was stated in section I that stimulating the cerebral cortex produces primary afferent depolarisation in the spinal cord and will inhibit both the spontaneous and evoked discharges of dorsal horn cells in the lumbo-sacral spinal cord.

Brown and Short (1974) and Brown, Coulter, Rose, Short and Snow (1977) have shown that hind limb spino-cervical tract units may be most efficiently inhibited from discrete areas of the contralateral hind limb sensory receiving area, S.I and also from the hind limb part of the second sensory receiving area, S.II.

Brown and Short (1974) observed that those areas of sensory cortex from which inhibition was most profound corresponded with those with commissural interconnections. Thus it was of interest to know if the ipsilateral sensory cortex has any inhibitory influence on spino-cervical tract cells.

Recently it has been reported (Cole and Gordon, 1976) that the cuneate nucleus receives corticofugal inhibition at a shorter latency than the gracile nucleus. Whether there is a similar temporal discrepancy in forelimb and hind limb information processing in the spino-cervical system is not known.

It was shown in section II that the 'hair only' light tactile receptive fields were relatively more important in the forelimb component of the spino-cervical tract. That these units may receive preferential treatment in the spino-cervical system was suggested after a comparison of the input and output of the lateral cervical nucleus. It would be interesting to know if these units receive the same corticofugal influence as other units.

METHODS

The experiments were performed on nine cats of either sex, weighing between 2 and 3.5 kg. Anaesthesia was produced by placing the animal in a perspex box through which passed a mixture of 4% Halothane in 50% nitrous oxide and 50% oxygen. When the animal was unconscious it was removed from the box and the same anaesthetic applied through a face mask. As soon as a deep stage of anaesthesia, as judged by the absence of reflexes, flaccidity of the limbs and slow, deep respiratory movements had been attained, one of the external jugular veins was exposed and cannulated and a solution of α chloralose in 0.9% saline was administered. This solution was made by warming the saline to 80°C and dissolving 1% w.v. of α chloralose in it. This was then allowed to cool but not to precipitate, and then a volume was slowly injected such that the cat received 70 mg for each kg of its body weight. The percentage of Halothane in the gaseous anaesthetic was then slowly reduced and removed altogether as soon as the chloralose took effect. The trachea was then cannulated with a Y tube which could later be attached to a respiratory pump and one of the carotid arteries was cannulated so that the blood pressure could be monitored. The wound at the throat was then closed with stitches and the cannulae were also secured to the skin with stitches.

An incision was then made in the skin of the head and the rostral skull was cleared of connective tissue, muscle and epichondral tissue. Cotton threads were sewn through

the edges of the skin incision so that it could be reflected when the cortex was later exposed on the frame.

The animal was next subjected to the same surgical procedures as described in section II, (i.e. laminectomy, bilateral pneumothoraxes and dissection of the four peripheral nerves), and transferred to the frame where it was secured as before. The skull over the sensorimotor cortex was then carefully trephined and bleeding from the bone was stopped with plasticine. Care was taken to avoid damage to the dura mata during trephining and the area of the brain was exposed further with bone clippers. In six cats the contralateral cortex (the cat's right hemisphere) only was exposed and in the remaining three a contralateral exposure was also performed. In these three cats the bone of the skull bordering on the sagittal suture was left intact to prevent damage to the superior sagittal sinus.

The dura mata was then cut away with fine iridectomy scissors and watch-makers' forceps and the surface of the cortex was photographed together with a scaled marker. At all times the cortical surface was kept moist with 0.9% saline solution at 38^{o}C applied on cotton wool swabs. When the photography had been completed the cortex was covered with a vaseline-paraffin mixture at 38^{o}C. This was viscous enough to adhere to its surface and thus prevent dehydration but allowed the passage of a fine sprung platinum ball electrode (Diam. 0.7mm). In the three experiments in which glass micropipettes were used as stimulating electrodes the pia mata on the surface of the cortex was removed, under

microscopic observation, with two pairs of watch-makers' forceps. A silver wire 'indifferent' electrode was placed in the temporal muscle.

The neck was stretched and the head flexed, as in section II, and an earthed silver wire inserted in the muscles of the neck prior to covering the exposed spinal cord with liquid paraffin. The mean arterial blood pressure was maintained above 70mmHg with the Dextrans solution described previously when necessary. The respiratory volume was adjusted so as to produce constricted pupils which resulted in an end tidal CO2 of between 3.6% and 4.4%. The animal was periodically allowed to recover from the gallamine triethiodide paralysant and if the level of anaesthesia appeared to be wearing off a supplementary dose of 30mg/kg α chloralose was given.

Recording techniques

The cord dorsum potential was recorded with a sprung platinum ball electrode and amplified by a Tektronix 122 preamplifier (Band pass filters set at 0.2 Hz and 1.0 KHz.) and displayed on a Tektronix 565 dual time base oscilloscope. The position of the maximum amplitude 'N' wave for an orthodromic superficial radial nerve volley was determined and under the operating microscope an incision was made in the pia mata at this position with two pairs of fine watchmakers' forceps. This was usually between the spinal segments C5 and C6. Through the incision glass micropipettes could be driven. The pia mater in the cervical spinal cord

was found more difficult to cut than in the lumbosacral cord as reported previously by Dilly, Wall and Webster (1968).

Unitary recordings were made with glass micropipettes of 5-20MΩ impedance (at 1000Hz) filled under pressure with a saturated aqueous solution of procion yellow or procion red. Where necessary the tips were broken by light contact with tissue paper. Such electrodes were found easier to make and gave clearer recordings than pipettes filled with 3M NaCl.

Unitary potentials were led through a negative capicitance head stage and a pre-amplifier both made in the Department of Veterinary Physiology. The micro-electrode recordings were initially made with amplifier band pass frequencies of 60Hz and 2.5kHz. As the electrode was driven through the cord the ipsilateral dorsolateral funiculus was stimulated at C3 with a pair of bipolar silver stimulating electrodes and the area of maximum antidromic field potential was found. This area contained the majority of the spino-cervical tract cells encountered and its depth location was noted. The electrode was driven through 4,000 μm from the midline of the dorsal columns at an angle of 15^{o}-20^{o} to the vertical, so as to sample as much as possible of the dorsal horn. The area of maximum field potential was usually between 1500 and 2300 μm from the surface.

The band pass frequencies of the preamplifier were then changed to 200 HZ. and 4.5 kHz in order to minimise the field potential and hence clarify the unitary action potentials.

Extracellular action potentials were recognised by

their biphasic morphology (Amassian, 1953). Once an extracellular spike was located the electrode was removed and then redriven through the cord 50 μM medial, lateral, rostral or caudal and parallel to the original tract. In this way the extracellular spike was maximised to an amplitude of at least 1 mV), and single units could be held for long periods of up to four hours which was necessary for cortical grids to be made. A similar method was employed by Hongo, Jankowska and Lundberg (1968) for locating S.C.T. cells prior to penetration.

The cerebral cortex was stimulated with a platinum sprung ball electrode mounted on a micro-manipulator. The position of each stimulus point was located under the operating microscope and marked on the photograph. The surface geometry of the sulci were traced on to white paper and inhibitory maps drawn. Care was taken not to stimulate on blood vessels or near the cut edges of the dura mata as this was known to decrease motor thresholds by an order of magnitude (Livingston and Phillips, 1957).

The current passed was measured as the potential difference across a 10 KΩ resistor placed on the return path to earth. This potential difference was amplified by a Tektronix differential amplifier and displayed on one beam of the 565 oscilloscope. The input capacitances of the two sides of the amplifier were equalised with Tektronix P6006 x 10 attenuator probes.

In one experiment a bipolar cortical electrode (two platinum ball electrodes) was used in an attempt to obtain

better resolution in the inhibitory maps. However this was not achieved. Similarly movement of the indifferent electrode, usually the anode, had little or no effect on the level of inhibition. For the pupose of mapping the inhibitory areas of the cortex, stimuli consisted of bursts of three or four 0.2 ms, 1.0 m.A. or 2.0 m.A. pulses at 500 Hz. commencing 30-35 ms. prior to the superficial radial nerve stimulus.

In three experiments glass micropipettes of 0.5 - 1.0M Ω impedance filled with 3M NaCl were used as stimulating electrodes bursts of 6, 0.2 ms 500 Hz, 25 μA, 50μA, or 100μA pulses (cathodal) were used. This was later decreased to bursts of three 50 or 25μA pulses of the same duration and frequency.

An Ampex PR-500, 7 channel tape recorder was used to record

(1) micro-electrode potentials
(2) current monitor potentials
(3) trigger pulse for the oscilloscope
(4) trigger pulse for the S.R.N. stimulus
(5) time scale.

The later three pulses were taken directly from the Devices 'Digitimer' which triggered a pulse generator which in turn triggered the isolated stimulators.

At the end of the experiments in which depth stimulation was used the animal was killed with an overdose of Nembutal and perfused first with 0.9% saline to rinse away blood and then with 10% formol saline. The following day the cortex

was removed and immersed in 10% formol saline prior to sectioning.

For the surface stimulation experiments each stimulated point was located as described earlier. Once those areas eliciting inhibition had been roughly defined they were stimulated in finer detail in order to achieve greater resolution in the inhibitory maps. Before looking for S.C.T. units the locations of the forelimb receiving areas S.I and S.II were found by using the sprung ball stimulating electrode, which was shielded to earth, for recording cortical evoked potentials in a similar manner to that used for the cord dorsum potentials. Due to the convulsive nature of the anaesthetic, chloralose, electrical stimulation of the four exposed peripheral nerves was not always satisfactory, as widespread short latency surface positive potentials of inconsistent amplitude , followed by complex after-potentials were seen. This was particularly evident when the contralateral superficial radial nerve was stimulated. Natural stimulation of the contralateral limbs was thus used to locate the first and second somaesthetic receiving areas. The latter was also identified by ipsilateral skin stimulation. In two experiments the more caudal auditory cortex was identified by a surface positive evoked response to a hand clap.

Figure 15

A This photograph, taken at the start of an experiment, is of a bilateral cortical exposure with the grid marker used in all the experiments. 1 small division of the grid = 1mm.

B This is a tracing of the above photograph. Forelimb and hind limb 1st and 2nd sensory receiving areas, SI and SII, were determined with natural stimulation of the forepaw and hind paw.

CS = Cruciate Sulcus

CG = Coronal gyrus

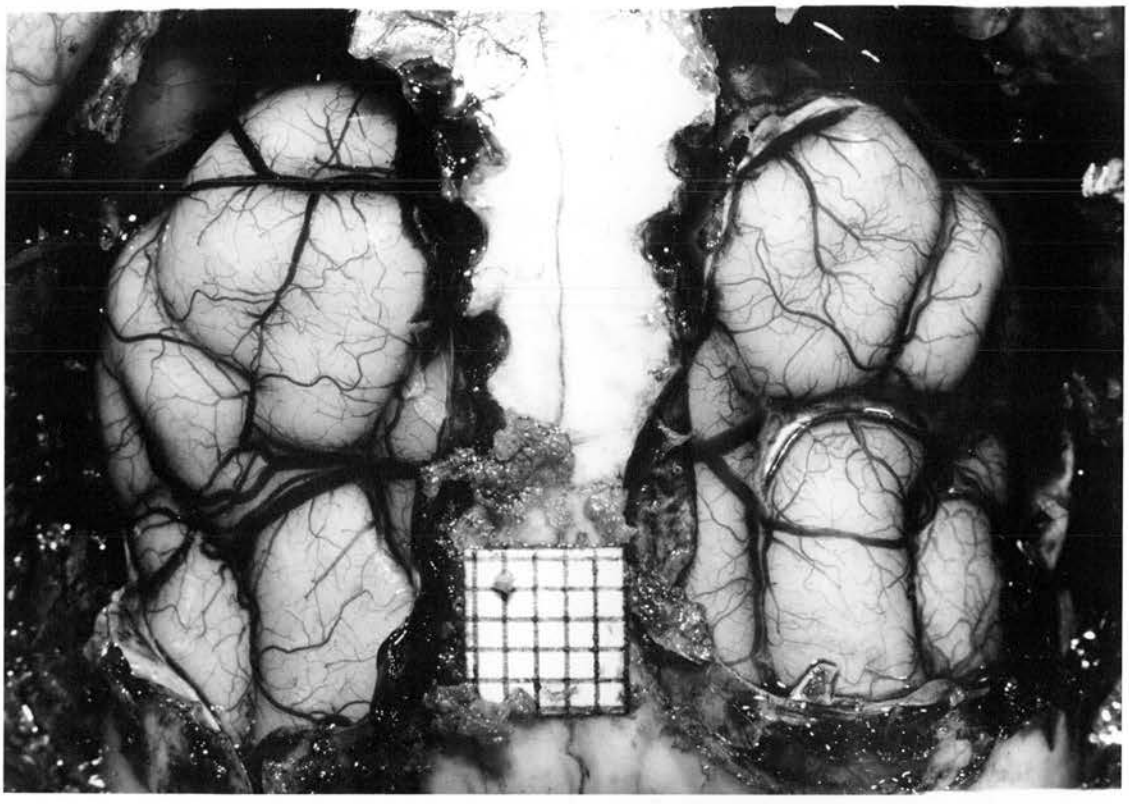
PSG = Post-sigmoid gyrus

ASG = Anterior suprasylvian gyrus

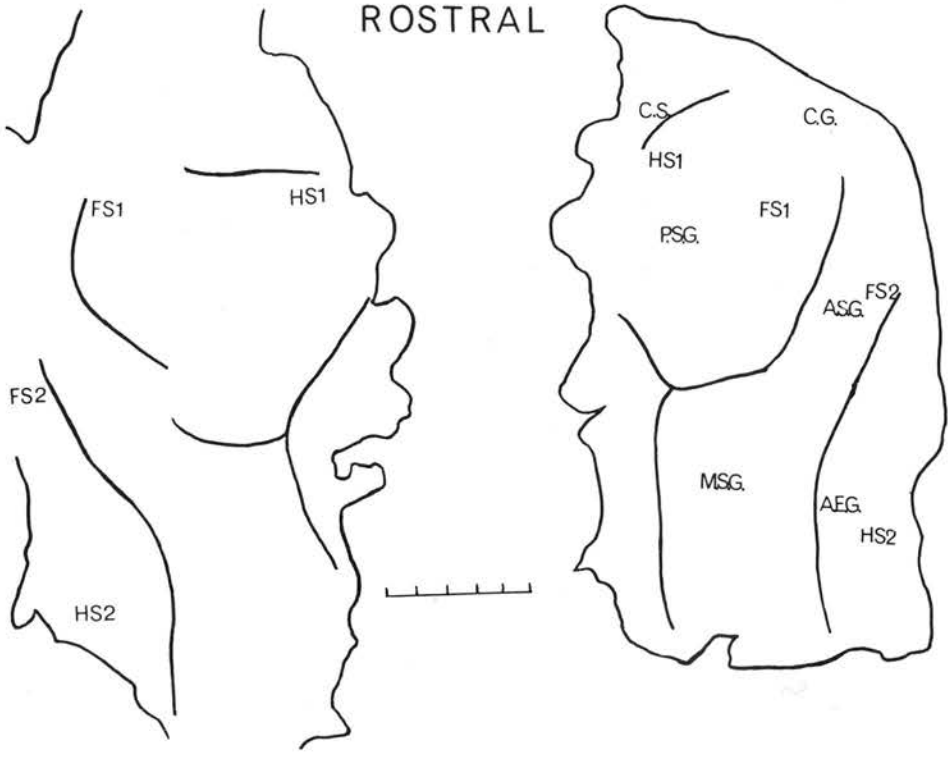
MSG = Middle suprasylvian gyrus

AEG = Anterior ectosylvian gyrus

A



B



Results

Evoked potential maps

Single shocks of 0.5 - 0.8 volts, which were slightly suprathreshold for producing the cord dorsum N wave, were used to locate the forelimb areas of the sensorimotor cortex. The corollary that the hind limb areas should be excited from the medial plantar nerves was also used to delimit the forelimb receiving area. (Figure 15)

The short latency surface positive response to electrical stimulation of the superficial radial nerve was observed at latencies of 4.8 - 6.4m.s. in the forelimb receiving area (Figure17).

The interval between shocks to the superficial radial nerve was 2.6 seconds. In some experiments the first positive wave was of variable amplitude after consecutive shocks and complex after potentials were seen. This was probably due to the use of chloralose as an anaesthetic (Woolsey, 1947).

Natural stimulation of the contralateral fore-paw was found to be a more convenient method of locating the fore-limb receiving area as a more discrete surface positive response resulted. The results of this method were used as the reference point when investigating corticofugal effects.

Slow wave studies

The area of the spinal cord giving a maximal cord dorsum potential (Negative wave) after stimulation of the superficial radial nerve was located at the beginning of each experiment.

Figure 16

A The conduction velocity histogram of the units of Section IV.

Mean = 51.64 ms^{-1}

Range = 25.5 - 80 ms^{-1}

Standard deviation = 17.4

B The conduction velocity histogram broken down into unit types.

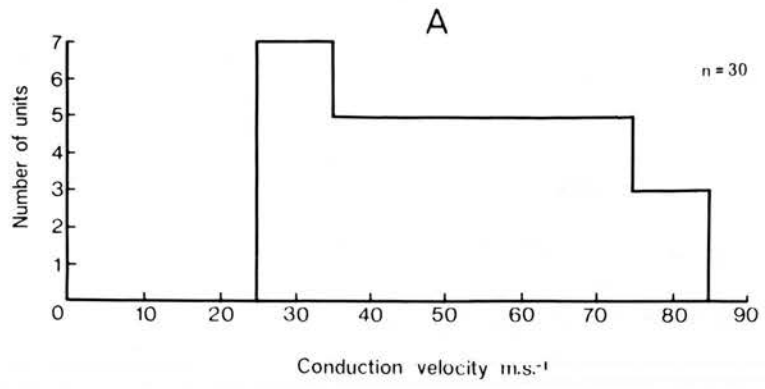
	Mean	Range	Standard Deviation
Hair	47.1ms^{-1}	25.5-80 ms^{-1}	17.6
Hair & pressure	61.3	45.5-85	13.3
Pressure	68.0		0
No R.F.	48.0		0

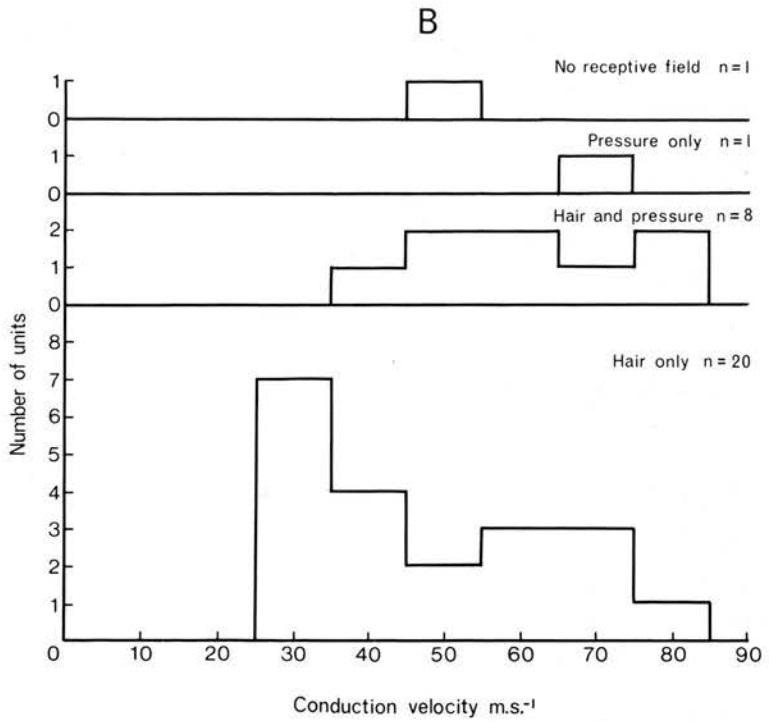
C Depth histogram. The depths of 16 SCT somata beneath the surface of the spinal cord was taken from the microdrive reading, which was set to 0 when the electrode tip was observed, under the dissecting microscope, to enter the white matter. No allowance was made for different angles of entry which varied from 15^{o} to 20^{o} to the vertical.

Mean = 2265 μm

Range = 1890-2600μm

Standard deviation = 245.7


A
n = 30
Number of units
0 10 20 30 40 50 60 70 80 90
Conduction velocity m.s.-1


B
No receptive field n = 1
Pressure only n = 1
Hair and pressure n = 8
Hair only n = 20
Number of units
0 10 20 30 40 50 60 70 80 90
Conduction velocity m.s.-1

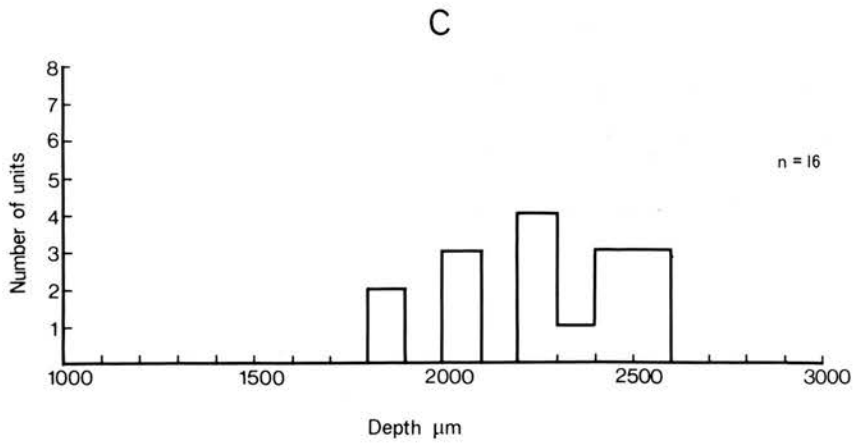

C
n = 16
Number of units
1000 1500 2000 2500 3000
Depth µm

Figure 17

A The potentials recorded from the surface of the cerebral cortex after stimulating the contralateral superficial radial nerve with a single, 0.2ms, 0.5 volt shock. The areas SI and SII are clearly demarcated. This cortex, 7542, was also stimulated to condition responses evoked in SCT cells by stimulation of the superficial radial nerve. See figures 20A and 26.

B Shows the evoked potential at SI at a greater magnification. The arrow shows the stimulus to the superficial radial nerve.

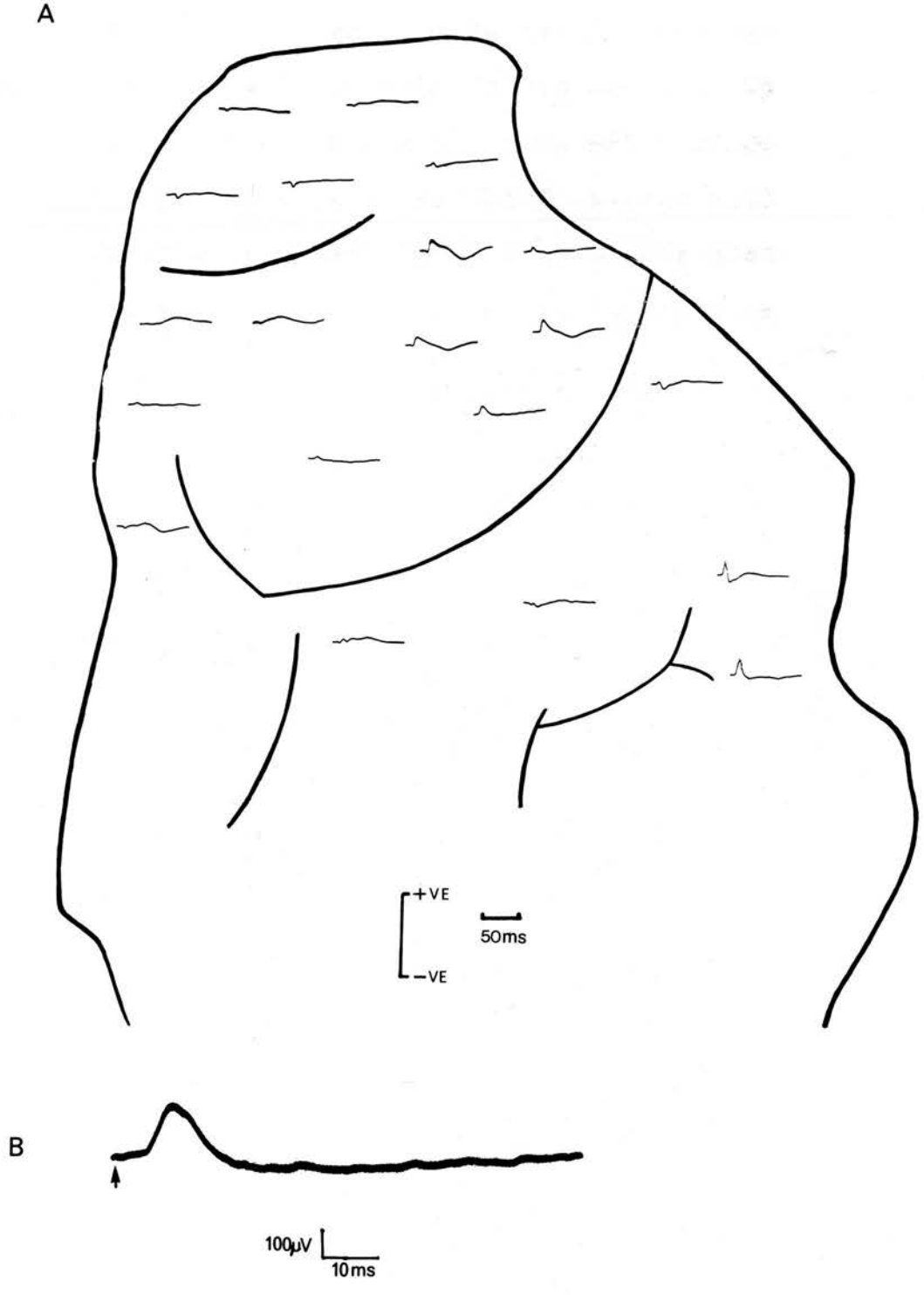

A
+VE
50ms
−VE
B
100μV
10ms

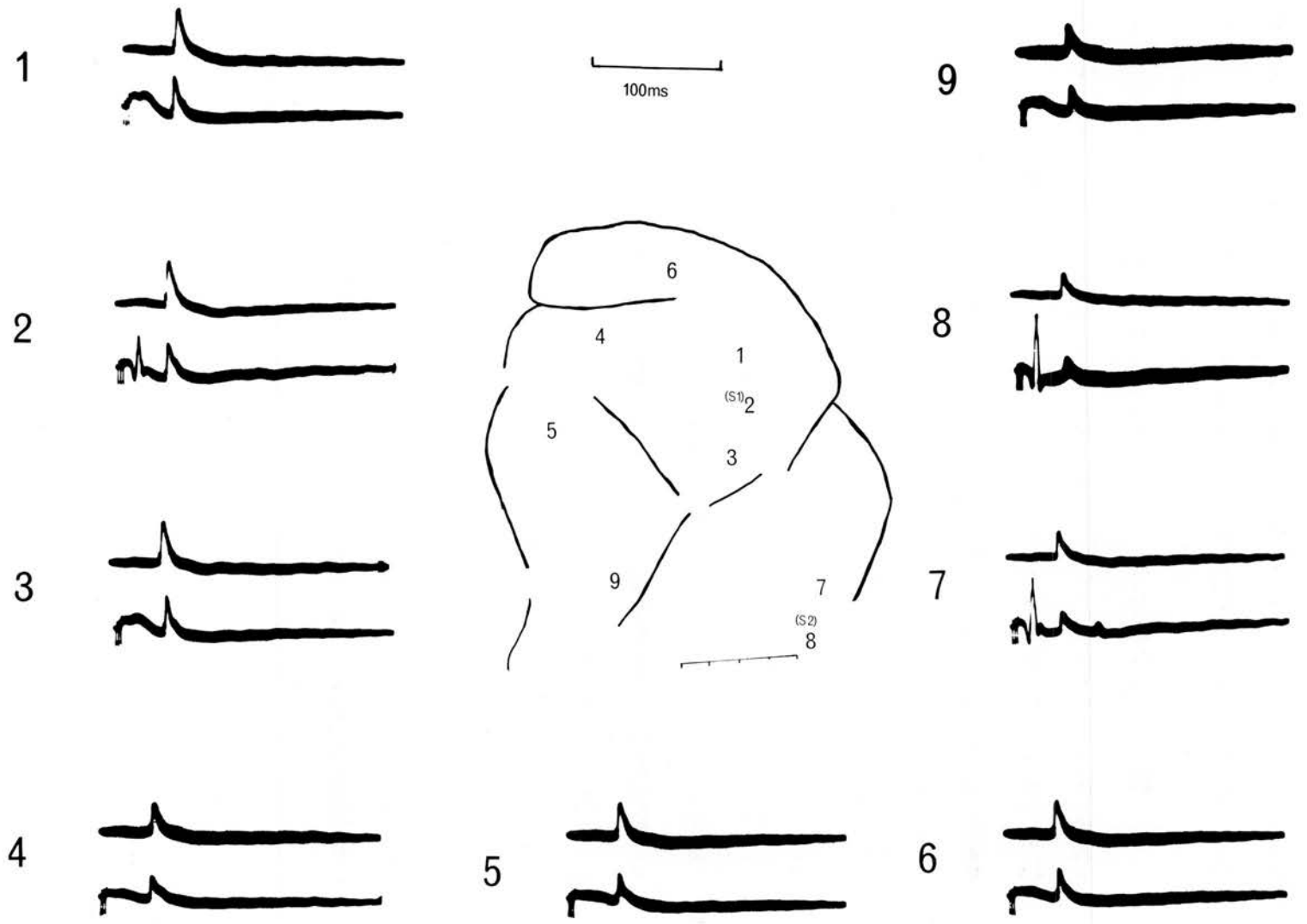
Figure 18

Contralateral cortex 7540 was stimulated to condition mass potential evoked on the cord dorsum by stimulation of the ipsilateral superficial radial nerve.

The top recording in each pair is the cord dorsum potential recorded in the spinal segment C5 - C6 after a 0.6 volt, 0.2ms shock to the SRN. The lower recording in each pair is the cord dorsum potential conditioned by a burst of 3, 0.2 ms 2.0 mA surface cathodal pulses, commencing 35 ms before the test stimulus to the SRN.

The numbers on the cortical outline refer to the position of the conditioning stimulus. The cortex was stimulated at points 1-9 sequentially and at each point a control recording of the cord dorsum potential was taken as there was some attenuation of the N wave probably due to the use of 4.0 mA conditioning pulses (not shown).

Note the early negative deflection of the cord dorsum potential in traces 2, 7 and 8. This could be caused by corticofugal fibres.


1
100ms
9
2
6
4
1
(S1)
2
5
3
8
3
9
7
(S2)
8
7
4
5
6

This was always rostral to the C7 entry zone and in 6 experiments was between the 5th and 6th cervical dorsal rootlets.

In two cats attempts were made to decrease the amplitude of the N wave and to produce an increased P wave by conditioning a slightly supramaximal stimulus for the N wave with a burst of 3 or 4, 500 Hz. 0.2ms pulses applied to the cerebral cortex. It was found that current strengths of 2.0mA produced a slight attenuation of the N wave and an increase in amplitude of the P wave. If the current strength was increased to 4.0 mA the effects on the N and P wave were increased.

Only the contralateral cortex was investigated in this fashion. The forelimb receiving area was most effective when 2.0 mA pulses were employed but effects were also elicited from the hind limb cortex when the current strength was raised to 4.0 mA. The interval between the cortical and peripheral stimuli was 35 m s as this time interval was known to give maximal inhibition of single units (Figure18).

Identification of spino-cervical tract units

In order to obtain recordings from spino-cervical tract units for sufficient time to map the cortical surface for inhibitory areas the cells of origin rather than the axons of the spino-cervical tract were chosen for study. This excludes the possibility of recording from dorsal spino-cerebellar tract units but increases the likelihood

of recording from either interneurones or the cells of origin of the forelimb homologue of the dorsal spino-cerebellar tract. For this reason units were identified on the criterion of collision in addition to the criteria used in section II. Electrical or natural stimulation of primary afferent fibres was used to produce an ortho-dromic train of impulses which would collide with the antidromic impulse.

From 9 experiments 30 units were studied. All were identified spino-cervical tract cells whose receptive fields could be typed as belonging to one of the categories described in Section II.

All the units could be excited by stimulation of the superficial radial nerve. The number of impulses evoked in the units by a single shock to this nerve was found to be a function of the stimulus voltage as was sometimes the latency of the first impulse. So as to obtain consistent numbers of impulses in consecutive trains the superficial radial nerve was stimulated at a strength which was just suprathreshold for eliciting a constant number of impulses in a train. This entailed using stimulus strengths ranging from 0.3 to 2.2. volts.

Even so slight fluctuations existed in the number of impulses in each train. Thus it was necessary to define inhibition as a statistically significant decrease in the mean number of impulses in a cortically conditioned train as compared to the unconditioned train. The significance test used was a small sample Students t test (Fisher, 1963)

performed on a Texas SR56 programmable calculator. For each point of the cortex examined for corticofugal influences five or more trains of both conditioned and unconditioned impulses were used. Thus if the excitability of the cell being studied changed during the recording period, which could be as long as four hours, some correction was made for this as the ratio of the mean number of conditioned to unconditioned impulses at each point was used to calculate the percentage inhibition. Similarly when inhibitory maps of the cortical surface were plotted for current strengths of 1.0mA and 2.0mA each point was stimulated at both current strengths before progressing to other cortical points. Thus if the physiological condition of parts or all of the cortex deteriorated during an experiment, this was reflected as evenly as possible in both maps.

Depth of spino-cervical tract units

Recordings were made of the microdrive depths at which 16 of the spino-cervical tract cells were encountered. The mean depth below the surface of the spinal cord was 2,265 μM with a range of 1890 - 2600 μM and a standard deviation of 245.7. No allowance was made for different angles of entry into the spinal cord, which varied from 15^{o}-20^{o} to the vertical, or for different thicknesses of the spinal cord in different cats (Figure16).

There was no relationship between the depth of a unit, the type or location of its receptive field and the

corticofugal influences acting upon it. However it would appear that spino-cervical tract cells in the cervical cord occupy a discrete part of the dorsal horn. This has been shown in the lumbo-sacral cord by the more accurate method of staining with intracellular procion yellow and horse-radish peroxidase (Brown, House, Rose and Snow, 1976a; Brown, Rose and Snow, 1977a).

Single unit studies

Recordings were made from 30 identified spino-cervical tract units whose receptive fields were on the distal forelimb and which were excited by stimulation of the cat's left superficial radial nerve. The mean conduction velocity of the sample was 51.64 ms^{-1} with a range of 25.5 - 80 ms^{-1} and a standard deviation of 17.4.

The latency of the first orthodromic action potential elicited by stimulation of the superficial radial nerve ranged from 2.9 ms to 5.4 ms. As the conduction distance was approximately 15 cm and Bromberg and Whitehorn (1974) have found that hair receptors have primary afferent fibres in the superficial radial nerve with conduction velocities ranging from 34-94 ms this would thus leave between 0.4 ms and 2.9 ms for synaptic delay if a unit was excited by primary afferent fibres with conduction velocities of 60 ms^{-1}. Thus it is posible that some of the spino-cervical tract units studied were not monosynaptically excited from the superficial radial nerve.

It is known from the results of section III and from previous workers (Brown, Kirk and Martin, 1973) that the presence of segmental inhibitions is a good indicator of the physiological state of the nervous system. Thus the contralateral superficial radial nerve and the medial plantar nerves were used to condition trains of action potentials elicited by stimulation of the ipsilateral superficial radial nerve. Inhibition was seen from the contralateral superficial radial nerve but never from the medial plantar nerves.

The receptive fields of 30 identified spino-cervical tract cells were classified into hair only, hair and pressure, pressure only and no receptive field types.

Hair only units

This type of unit was again the most frequently encountered and accounted for 66% of the sample (20 units). Seven of these units were examined under the operating microscope as described in section II. Six were found to be excited by movement of tylotrich hairs and one by movement of guard hairs without a pressure component. Thus this group of units corresponded to groups I and II of Brown (1971). The mean conduction velocity of hair only units was 47.1 ms^{-1} with a standard deviation of 17.6 and a range of 25.5 - 80 ms^{-1} .

Eighteen out of the twenty units were inhibited by stimulating the forelimb receiving area of the contralateral cerebral cortex with 1.0mA or 2mA trains of pulses. Five

out of nine units tested could also be inhibited with trains of 2.0mA pulses applied to the forelimb receiving area of the ipsilateral cerebral cortex. None of the units which could not be inhibited from the cortex was subject to segmental inhibition.

Hair and pressure units

Eight units of this type were encountered. Their receptive fields were similar to those described in section II; a rapidly adapting response was evoked by brushing of hairs and a slowly adapting response by the application of a sprung clip. The mean conduction velocity of these units was 61.3 ms^{-1} with a range of 45-85 ms^{-1} and a standard deviation of 13.3. These units are similar to types II and III of Brown (1971).

Four out of the eight units were inhibited by 1.0 or 2.0 mA pulses applied to the contralateral forelimb receiving cortex and in four units no inhibition could be elicited from the cerebral cortex. Three of the units for which no inhibition could be found came from experiments in which hair only units were subsequently sampled which received inhibition from the cortical stimuli. The other unit was the last unit found in an experiment in which inhibition was present for the other units sampled. Only one of the units which received no corticofugal inhibition could be inhibited from the contralateral superficial radial nerve. One hair and pressure unit received corticofugal inhibition from the ipsilateral cortex.

Pressure only units

One unit of this type was found. Its receptive field was close to the superficial radial nerve stimulating electrode and it is possible that a hair component existed but was damaged during the dissection. This unit gave a slowly adapting response to application of a metal clip. Its conduction velocity was 68 ms^{-1}.

This unit was inhibited by 1 mA pulse applied to the forelimb receiving area of the contralateral cortex. It was not tested for inhibition from the ipsilateral cerebral cortex.

Units with no receptive field

One unit of this type was found. It was excited by stimulation of the superficial radial nerve and had a conduction velocity of 48.0 ms^{-1}. This unit was inhibited by 2.0 mA pulses applied to the forelimb receiving area of the contralateral cortex. It was not investigated in greater detail.

Inhibition elicited from the surface of the cerebral cortex.

There was considerable variation in the threshold current needed to elicit inhibition from the surface of the cortex. Current strengths needed to elicit statistically significant inhibition varied between 0.5 mA and 1.7 mA. Cathodal currents were more effective than anodal currents. Variations in the inhibitory threshold currents existed both between different cats and between different units

in the same cat.There was also considerable variation in the surface geometry of the cerebral sulci. In particular the post cruciate dimple was not always definable and the Ansate and Coronal sulci were sometimes continuous. For these reasons inhibitory grids of the cortex were plotted for uniform current strengths of 1.0 mA or 2.0 mA or both (Figures 20-24 and 28)

The interval between conditioning stimuli was 1.6 seconds. It was observed that if intervals of less than 0.6 seconds were employed the inhibition elicited was temporally inconsistent. In such cases inhibition was present in the first conditioned train but varied and was usually decreased in the four or more subsequent conditioned trains.

Inhibition from the cerebral cortex was observed on units in which the contralateral superficial radial nerve gave little, or in 5 units, no inhibition. Stimulation of the cortex with 2.0 mA pulses gave total inhibition in two units (there were no impulses in the conditioned train) whereas stimulation of the contralateral superficial radial nerve usually gave less inhibition and was never total even when trains of maximum voltage (10V) were used. However the two sources of inhibition did not summate in their effects when on two occasions both were used simultaneously as conditioning stimuli.

It was a common feature of the corticofugal inhibition from both hemispheres, that the inhibitory mechanism acted preferentially on the later impulses of the evoked impulse

Figure 19

This illustrates the way in which grids of corticofugal inhibition were mapped. These recordings are the data for a single point.

A 5 unconditioned responses of the SCT cell to electrical stimulation of the superficial radial nerve (arrows) with an 0.8 volt 0.2ms shock.

The 5 responses are now conditioned by a burst of 3, 500Hz 0.2ms,1.0 MA surface cathodal pulses applied to the cerebral cortex (contralateral forelimb SI area).

B 5 unconditioned responses as in A.

The 5 responses are now conditioned by a burst of 3, 500Hz 0.2ms 2.0 mA surface cathodal pulses applied to the cerebral cortex (contralateral forelimb SI area).

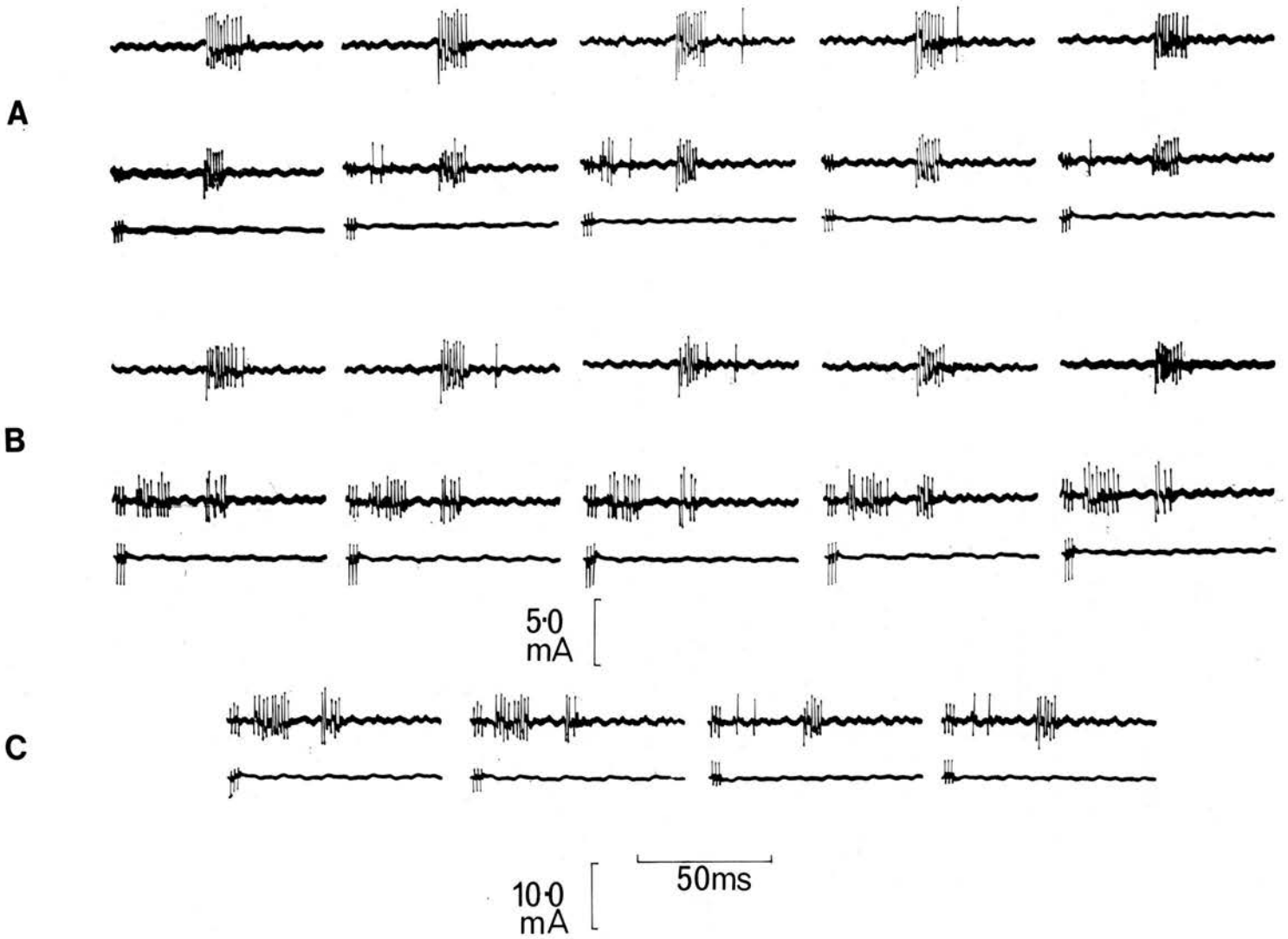
The significance of the inhibition was calculated with a small sample Students t test.

1.0 mA % inhibition = 33 $P < 0.01$

2.0 mA % inhibition = 51 $P < 0.001$

C Inhibition with 2.0 mA anodal and 2.0 mA cathodal pulses. Cathodal pulses give greater inhibition.

The conditioning testing interval is 33 ms in all traces.


A
B
5·0
mA
C
50ms
10·0
mA

train. The first action potential was only eliminated in two units which showed total inhibition. If the testing shock to the superficial radial nerve was increased beyond the strength needed to elicit the constant impulse train number then the inhibition elicited from a given cortical stimulus decreased.

Action potentials in spino-cervical tract cells following cortical stimulation

When the cortex but not the contralateral superficial radial nerve was used as a conditioning stimulus evoked trains of action potentials were frequently seen prior to the excitatory testing stimulus to the ipsilateral superficial radial nerve. Such action potentials were of variable latency, the earliest latency observed was 7.0 ms after the first conditioning impulse. They also occurred after conditioning stimuli were applied to the cortex without a subsequent testing stimulus. As many as 10 of these action potentials were evoked by a train of three cortical stimuli (Figure19). They were usually most frequent when those areas eliciting inhibition were stimulated but were observed in the absence of inhibition. These action potentials were seen in units with no spontaneous discharge and had a similar wave form and amplitude to impulses evoked by stimulation of the ipsilateral superficial radial nerve.

Of particular relevance to this phenomenon was the observation of a unit undergoing corticofugal 'mapping'.

This suddenly displayed an injury discharge consisting of a sudden fluctuation in membrane potential followed by a high frequency train of impulses. When extracellular recording was resumed the cell was hyperexcitable and displayed action potentials after stimulation of both cortex and ipsilateral superficial radial nerve. Prior to injury this unit could not be excited from the cortex.

Areas of the contralateral cerebral cortex eliciting inhibition

Of the 24 units that could be inhibited by stimulating the contralateral cortex, grids (defined as inhibition tested for at 9 or more cortical loci) were obtained for 14 units.

For a given stimulus strength inhibition was greatest from the first forelimb receiving area, S.I of Marshall, Woolsey and Bard (1941). The first and second face areas and the second forelimb area, S.II of Adrian (1941) also elicited inhibition at the same stimulus strength.

The hind limb receiving areas never gave significant inhibition when stimulated with 1.0 mA pulses but sometimes did when 2.0 mA pulses were used. In such cases the forelimb receiving areas gave a greater degree of inhibition.

The degree of inhibition, expressed as a percentage, was not related to the type of unit, its receptive field location on the forelimb, or the conduction velocity of its axon. However lack of inhibition was more common in 'hair and pressure' type units than 'hair only' units.

Figure 20

Figures 20-24 are grid maps of corticofugal inhibition of transmission through an SCT cell. The outlines of photographs of the cortex, taken at the start of the experiment (see Figure 15) were later traced out and marked, at the point of stimulation, with the degree of inhibition calculated as shown in Figure 19. Each division of the scale represents 1mm. All conditioning stimuli were trains of 3 or 4 500Hz 0.2ms surface cathodal pulses of 1.0 or 2.0 mA, commencing 30-35 ms prior to the test stimulus. The location of the receptive field of the unit under study is also shown. The forelimb SI and SII areas were determined with natural stimulation of the forepaw.

Figure 20 illustrates the discrete localisation of inhibition from the surface of the contralateral cerebral cortex.

A A 'hair only' (Tylotrich) unit inhibited with 1.0 mA pulses. Unit 754206

B A 'hair only' (Tylotrich) unit inhibited with 2.0 mA pulses. Unit 754105.

Open circles indicate inhibition of 10-19%

Dots indicate no inhibition,

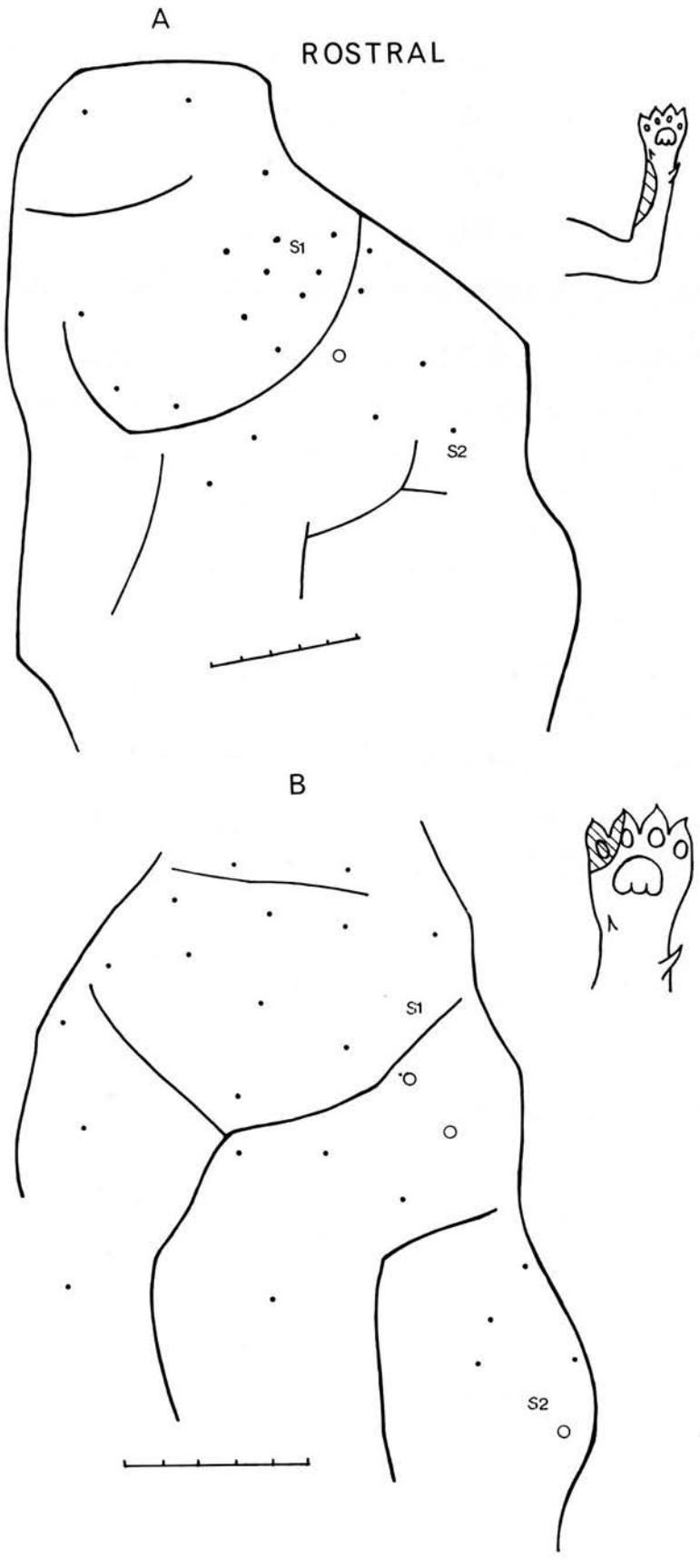

A
ROSTRAL
S1
S2
B
S1
S2

Figure 21

Unit 754002 'Hair only' receptive field

Grid map of corticofugal inhibition with:

A 1.0 mA pulses applied to the contralateral cerebral cortex

B 2.0 mA pulses applied to the contralateral cerebral cortex

Note the expansion of the inhibitory areas in B

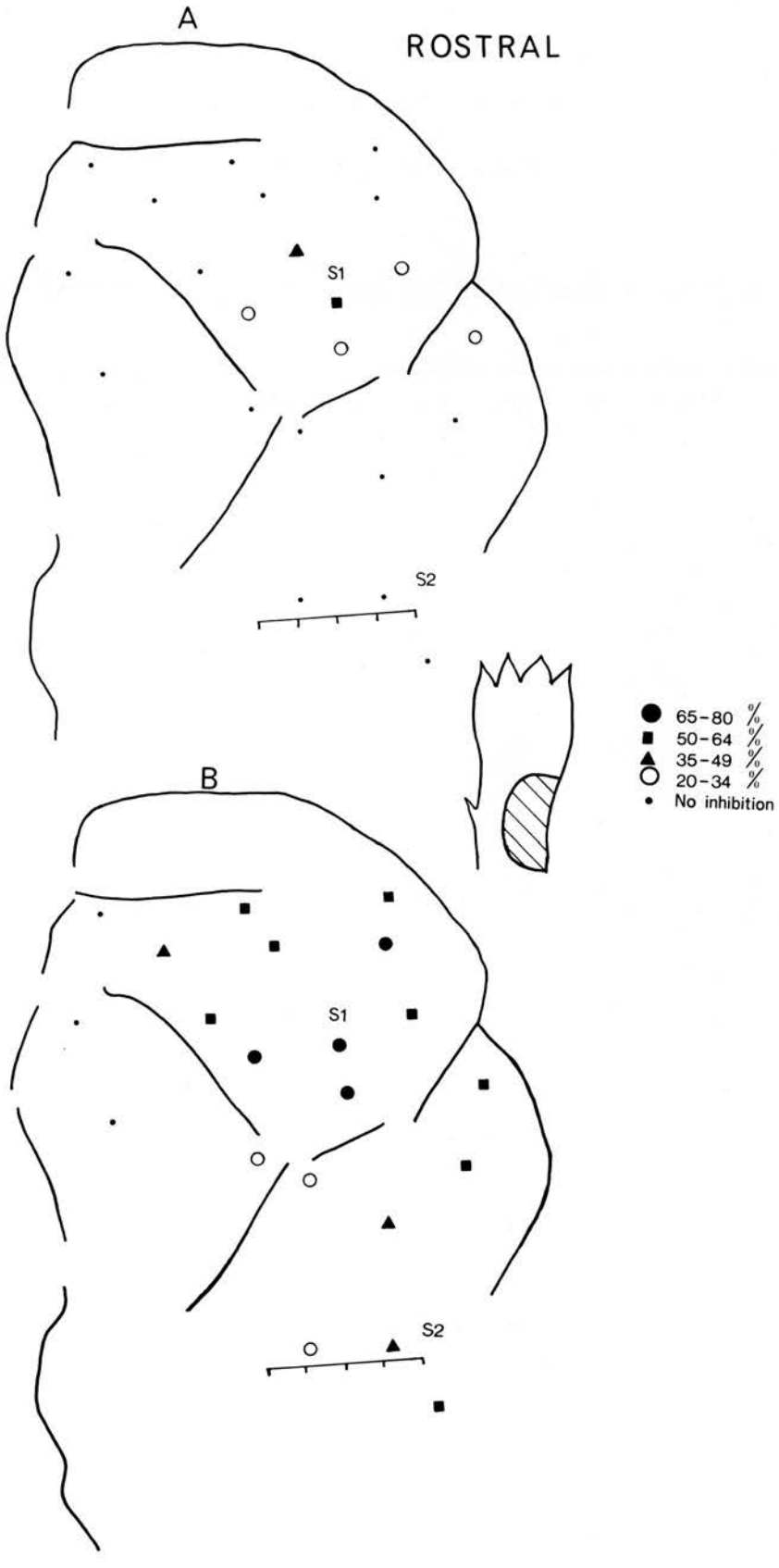

A
ROSTRAL
S1
S2
B
S1
S2
65-80 %
50-64 %
35-49 %
20-34 %
No inhibition

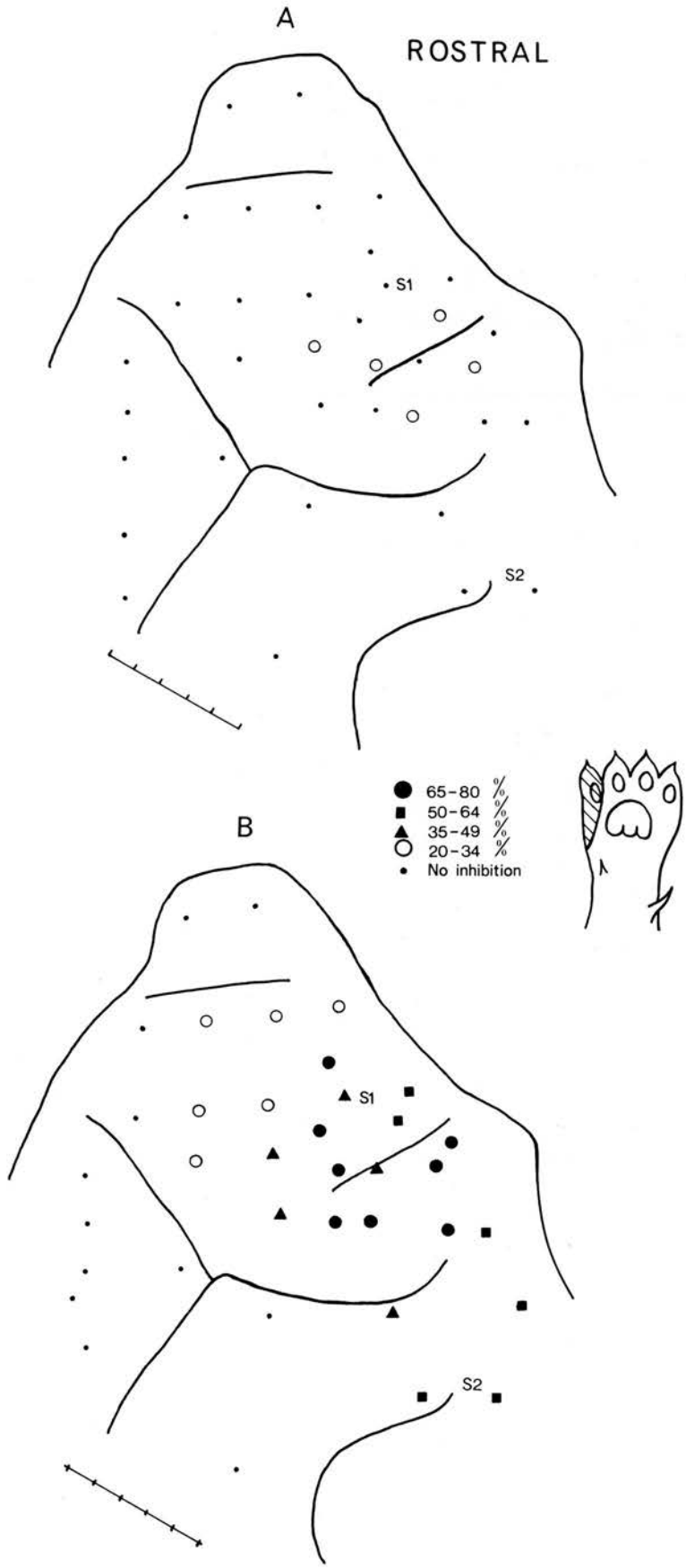
Figure 22

Unit 754301 'Hair only' type receptive field.

Grid map of coticofugal inhibition with:

A 1.0 mA pulses applied to the contralateral cerebral cortex.

B 2.0 mA pulses applied to the contralateral cerebral cortex.


A
ROSTRAL
S1
S2
65-80 %
50-64 %
35-49 %
20-34 %
No inhibition
B
S1
S2

For three experiments composite inhibitory maps were made by normalising the percentage of inhibition, for a constant conditioning current, with respect to the maximum and averaging the normalised values for the inhibition at various loci for a number of units. This revealed more clearly the somatotopic nature of the corticofugal inhibition and the relation of the inhibitory areas to the sensory receiving areas (See Figures 25-27).

The time course of inhibition elicited from the contralateral cortex

This was investigated by varying the conditioning-testing interval with the cortical stimulating electrode placed on an area known to give inhibition (Figure 29).

Inhibition from the forelimb S.I. area was greatest for a 30 ms interval between the beginning of the conditioning train and the testing stimulus. In the same unit inhibition from the forelimb S.II area peaked slightly later. Inhibition elicited from the hind limb S.I area with 2.0 mA pulses had a different time course and a more delayed onset. (Figure 30)

The duration of inhibition from the forelimb S.I area was considerable. For 3 units inhibition was still present after a conditioning testing interval of 200 ms.

Areas of the ipsilateral cerebral cortex eliciting inhibition.

Six out of eleven units which could be inhibited from the contralateral cortex could also be inhibited with 2.0 mA

Figure 23

Inhibition from both the contralateral and ipsilateral cerebral hemispheres.

Unit 762007 'Hair only' (Guard) type receptive field. This grid was obtained with 1.0 mA pulses.

From both hemispheres of the cortex the SI area appears to mediate more inhibition than the SII area.

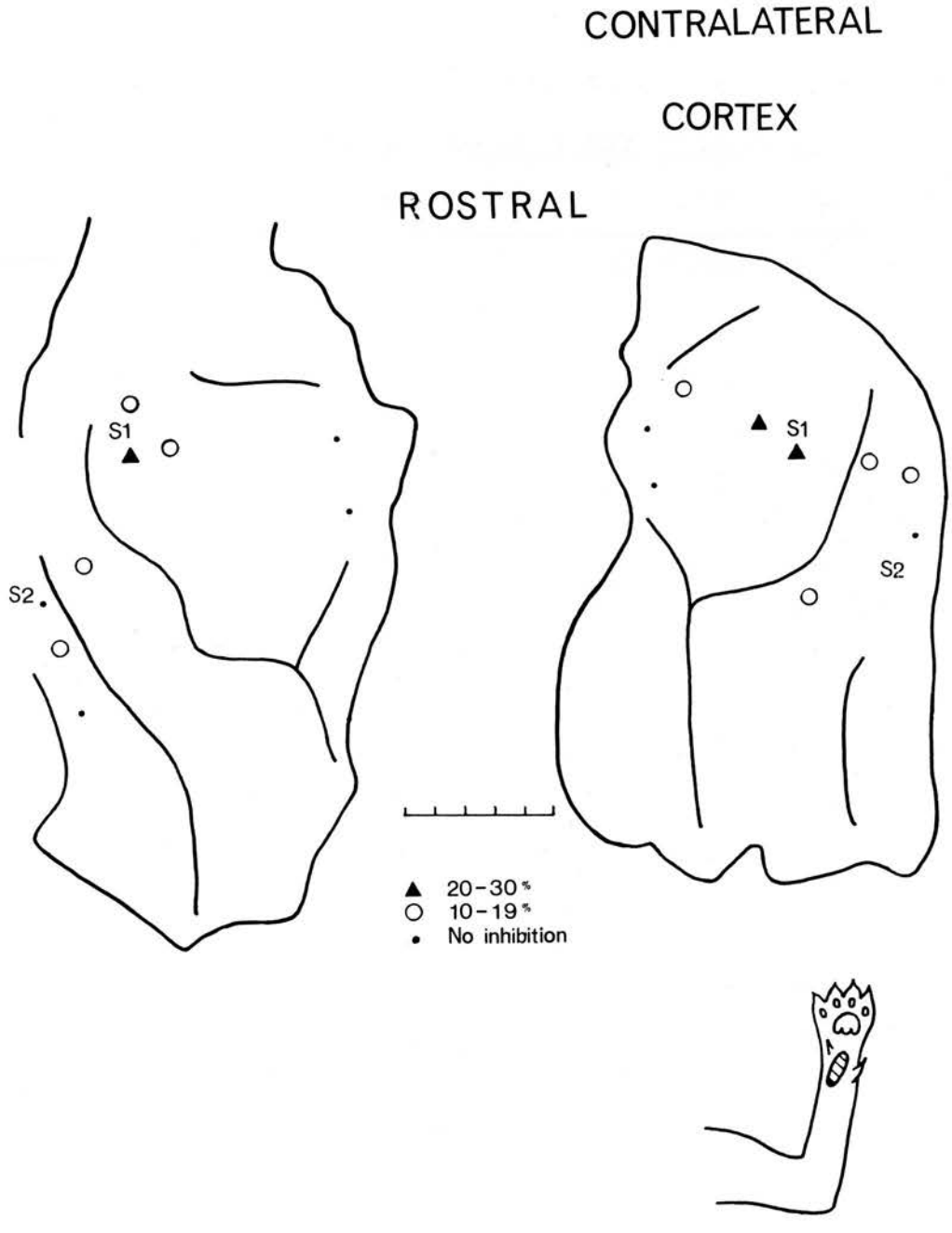

CONTRALATERAL
CORTEX
ROSTRAL
S1
S2
S1
S2
20-30%
10-19%
No inhibition

Figure 24

Inhibition from both the contralateral and ipsilateral cerebral hemispheres.

Unit 762004, 'hair only' type receptive field. This grid was obtained with 2.0 mA pulses.

Note the different values for inhibition in the key.

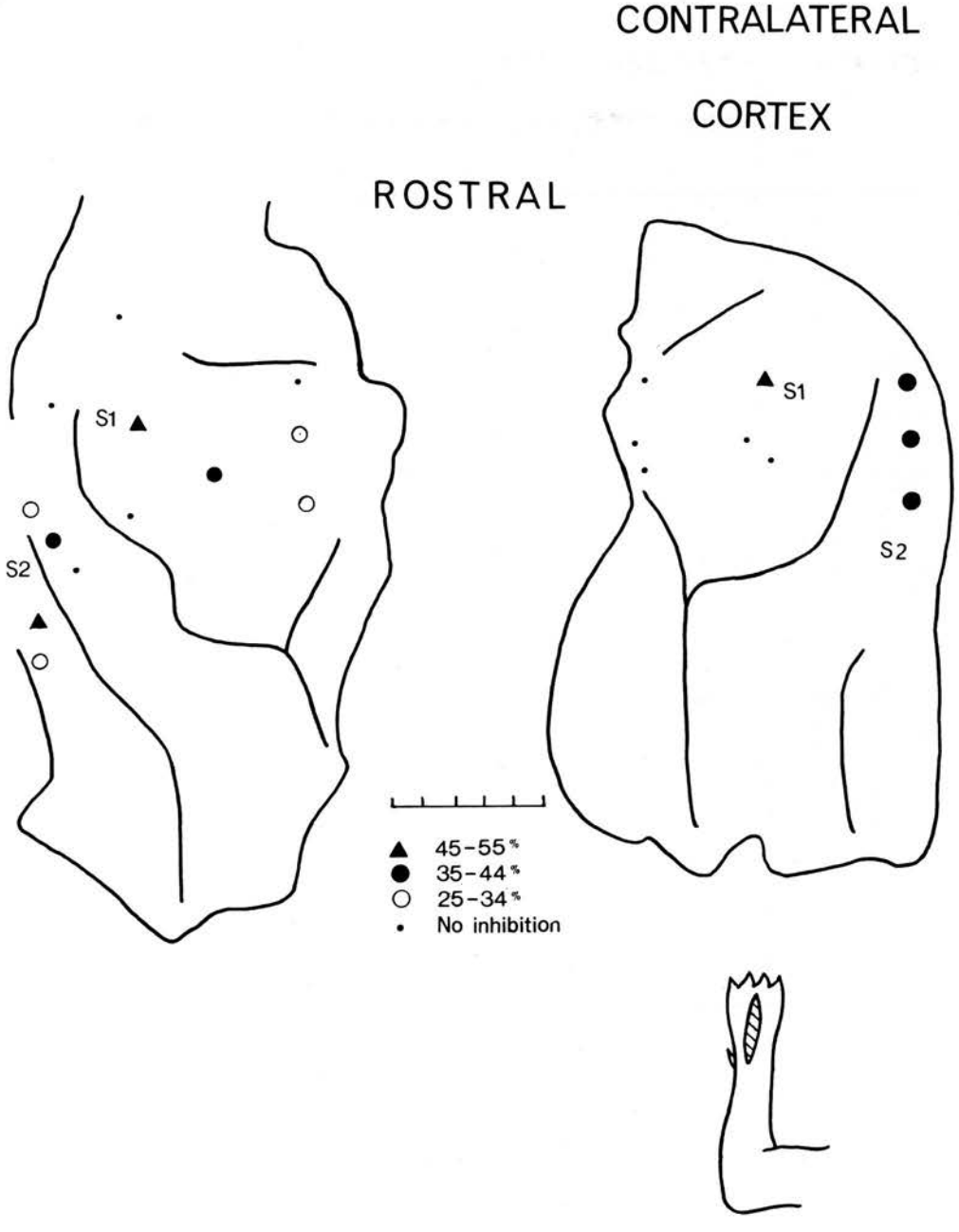

CONTRALATERAL
CORTEX
ROSTRAL
S1
S2
S1
S2
45-55%
35-44%
25-34%
No inhibition

Figure 25

Figures 25-27 show composite inhibitory maps. The areas of the contralateral cerebral cortex eliciting inhibition with 2.0 mA conditioning pulses were averaged for 3 or 4 units.

This was done by expressing the percentage of inhibition at each point as a percentage of the inhibition at the point which gave most inhibition on the unit under study. These 'normalised' values were then averaged over the 3 or 4 units for which inhibitory maps were plotted. Note the different keys of normalised inhibition used in the three figures.

Figure 25

Cortex of experiment 7541. The percentage of inhibition was normalised and averaged over 3 units. See figure 20B for the location of SI and SII.

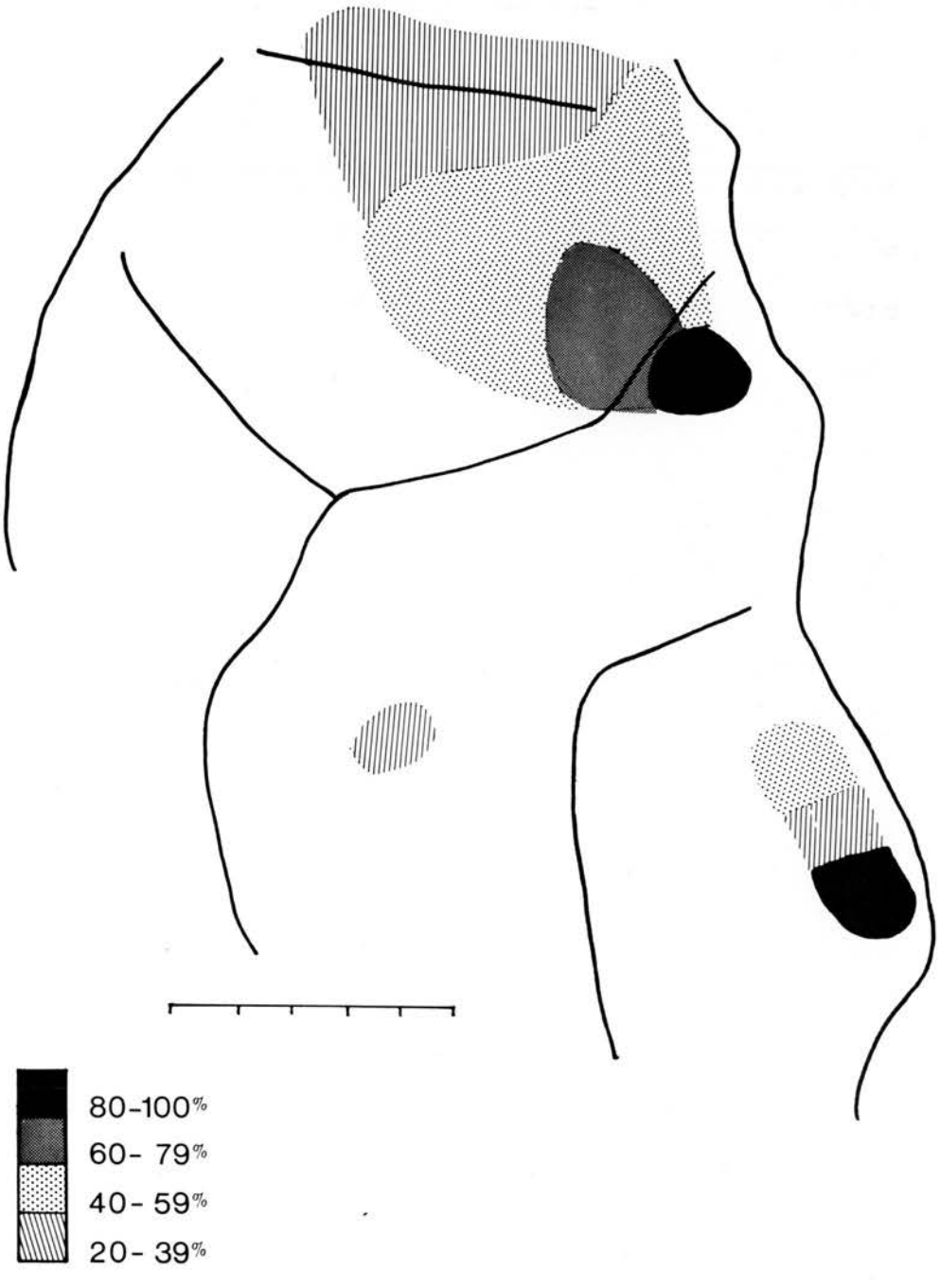

ROSTRAL
80-100%
60- 79%
40- 59%
20- 39%

Figure 26

Cortex of experiment 7542. The percentage of inhibition was normalised and averaged over 3 units. See figure 20A for the location of SI and SII.


ROSTRAL
90-100%
80- 99%
50- 60%

Figure 27

Cortex of experiment 7540. The percentage of inhibition was normalised and averaged for 4 units. See figure 21 for the location of SI and SII.

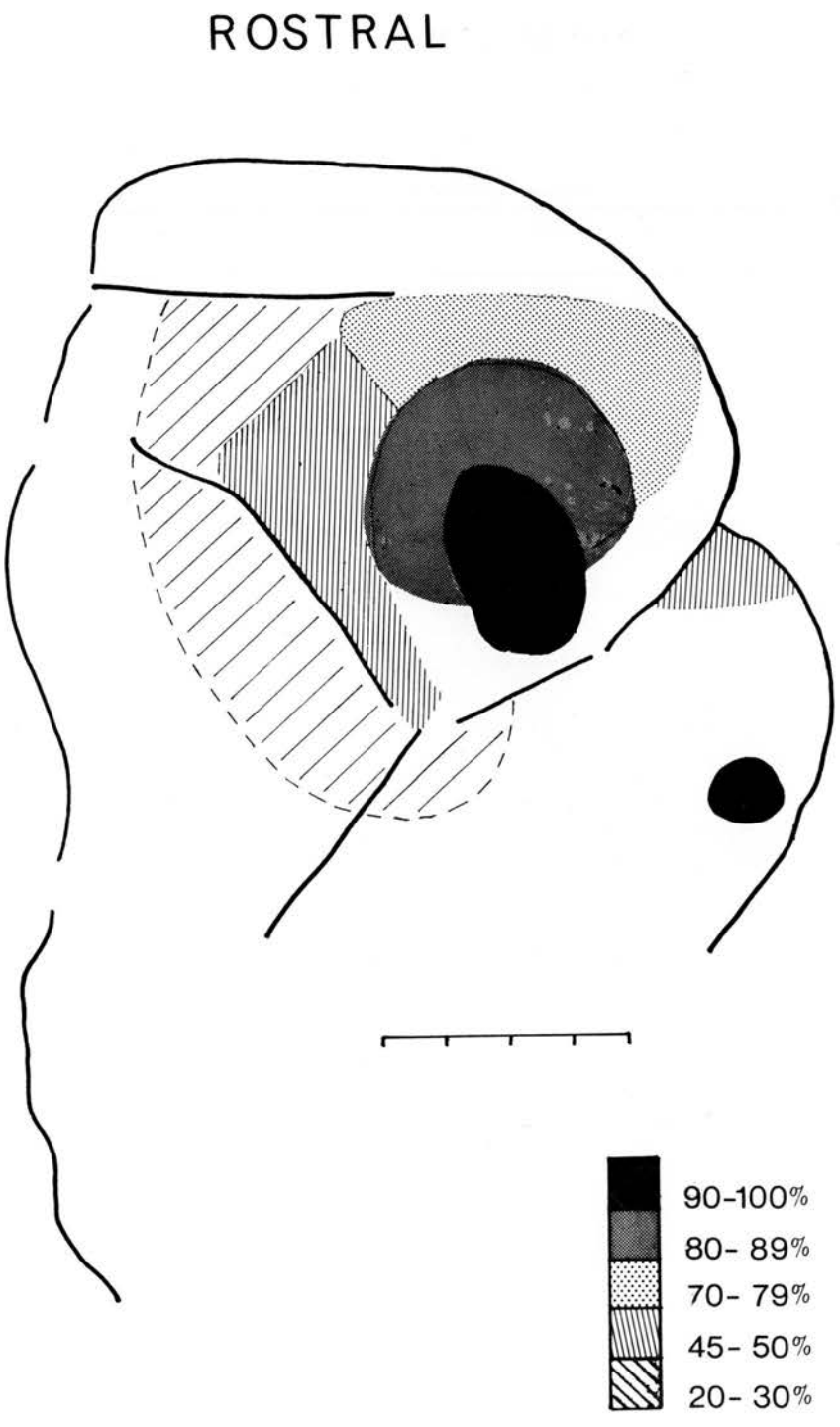

ROSTRAL
90-100%
80- 89%
70- 79%
45- 50%
20- 30%

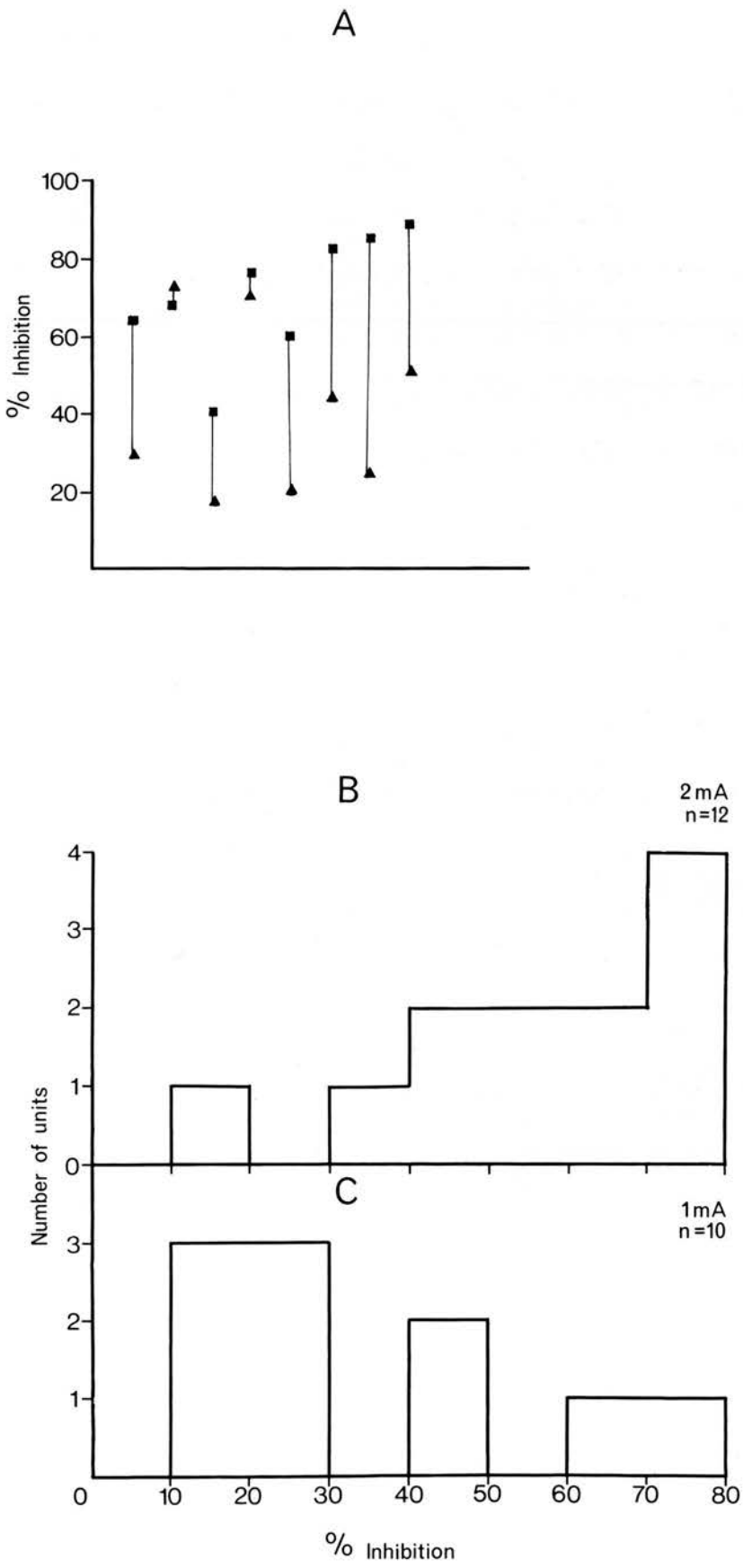
Figure 28

This illustrates the relationship between the conditioning current strengths and the degree of inhibition from the contralateral cortex.

A For the 8 units for which inhibitory grids were determined with conditioning current strengths of both 1.0 mA and 2.0 mA the percentage of inhibition, at the point of greatest inhibition, was plotted for 2.0 mA pulses with squares and for 1.0 mA pulses with triangles. A vertical line has been drawn between conditioning currents applied to the same unit.

B and C For the 12 units for which inhibitory grids were plotted with conditioning current pulses of 2.0 mA and for the 10 units for which inhibitory grids were plotted with conditioning current strengths of 1.0 mA the percentages of inhibition at the point giving greatest inhibition were plotted as a histogram.

	Mean	Range	Standard Deviation
B	36.5%	16-72%	21.2
C	57.5%	19-78%	18.4


A
100
80
60
40
20
% Inhibition
B
2 mA
n=12
4
3
2
1
0
Number of units
C
1 mA
n=10
3
2
1
0
10
20
30
40
50
60
70
80
% Inhibition

pulses applied to the ipsilateral cortex. All of the 5 units unaffected by 2.0mA conditioning stimuli were inhibited by 4.0 mA pulses.

Inhibitory grids were plotted for 4 units. Maximum inhibition was again found when the forelimb S.I. area was stimulated although the forelimb S.II area also gave some inhibition. In two units 1.0 mA pulses produced weak inhibition from the ipsilateral S.I area.

The time course of inhibition elicited from the ipsilateral cortex

For the same unit and for conditioning pulses of the same strength inhibition from the ipsilateral forelimb area S.II was weaker and later to peak than that from the ipsilateral forelimb area S.I. However inhibition from the ipsilateral S.I area was similar in its time course to that from the contralateral S.I area (Figure31).

The effects of ipsilateral hemisection of the spinal cord on corticofugal inhibition

In two cats the spinal cord was partially hemisected, at the C1 level ipsilateral to the recording electrode, with a blunt spatula. Prior to the hemisection the units under study received inhibition from the contralateral forelimb S.I area. This inhibition was released immediately following the hemisection. In both experiments the blood pressures fell (from 90 to 50 mmHg and from 75 to 45 mmHg) following the hemisection. However the fall in blood pressure was

gradual whilst the release in inhibition was immediate and thus probably attributable to interruption of fibres mediating the inhibition (Figure 32).

The effects of barbiturate on corticofugal inhibition

For one unit the effects on inhibition of the short acting barbiturate, sodium thiopentone, were investigated. 10mgm was injected intravenously and this eliminated inhibition five minutes after administration. However after 45 minutes inhibition had recovered to a significant level. There was a decrease in blood pressure of about 10mmHg immediately after the intravenous injection but the mean blood pressure remained constant for the next hour (Figure 32).

Stimulation of the cortex in depth

In three cats, which demonstrated corticofugal inhibition from their contralateral hemispheres after surface stimulation, micropipettes were used to stimulate the cortex in depth. The electrode was lowered by 125μM steps normal to the cortical surface. In the first cat a train of 6 100 μA stimuli were used and inhibition was seen consistently at stimulating depths of 1000 - 1850μM in the forelimb receiving area.

In the later two experiments inhibition was localised in each track by using 50 μA or 25 μA pulses. In one animal an area giving inhibition was found 1500μM beneath the post-cruciate dimple and in the other experiment two tracks in the more lateral forelimb cortex were found to give

Figure 29

The time course of inhibition of an SCT unit from the contralateral forelimb receiving area SI (left) and the contralateral superficial radial nerve (right) arrow.

A shows a test response to a 3.0 x threshold stimulus to the superficial radial nerve. The conditioning-testing intervals are:

B 12 ms

C 25 ms

D 33 ms

E 55 ms

F 80 ms

The conditioning stimuli were 3, 500 Hz, 0.2 ms, 2.0 mA pulses to the cortex and 3, 500 Hz 0.2ms 3 x threshold pulses to the contralateral superficial radial nerve.

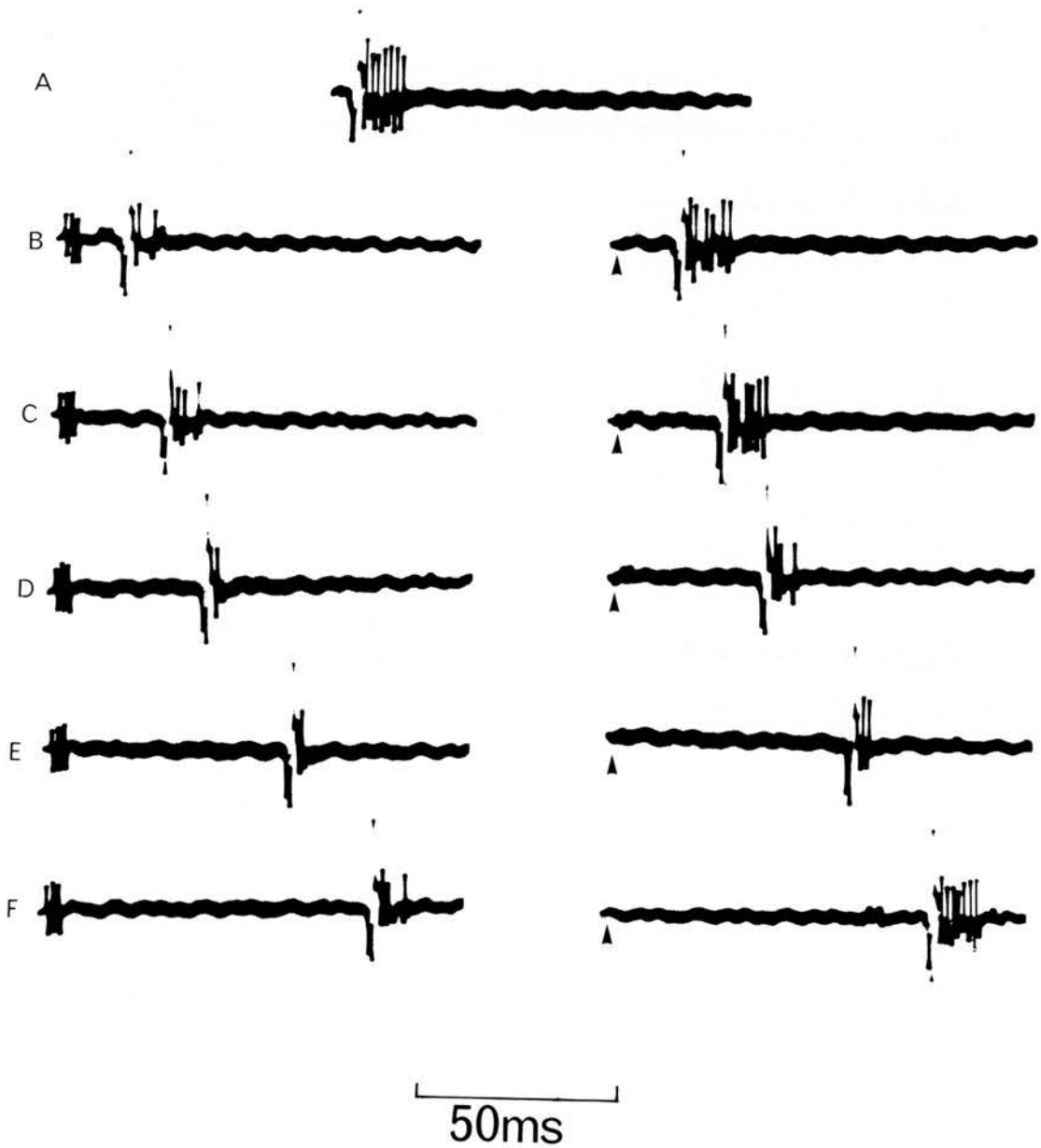

A
B
C
D
E
F
50ms

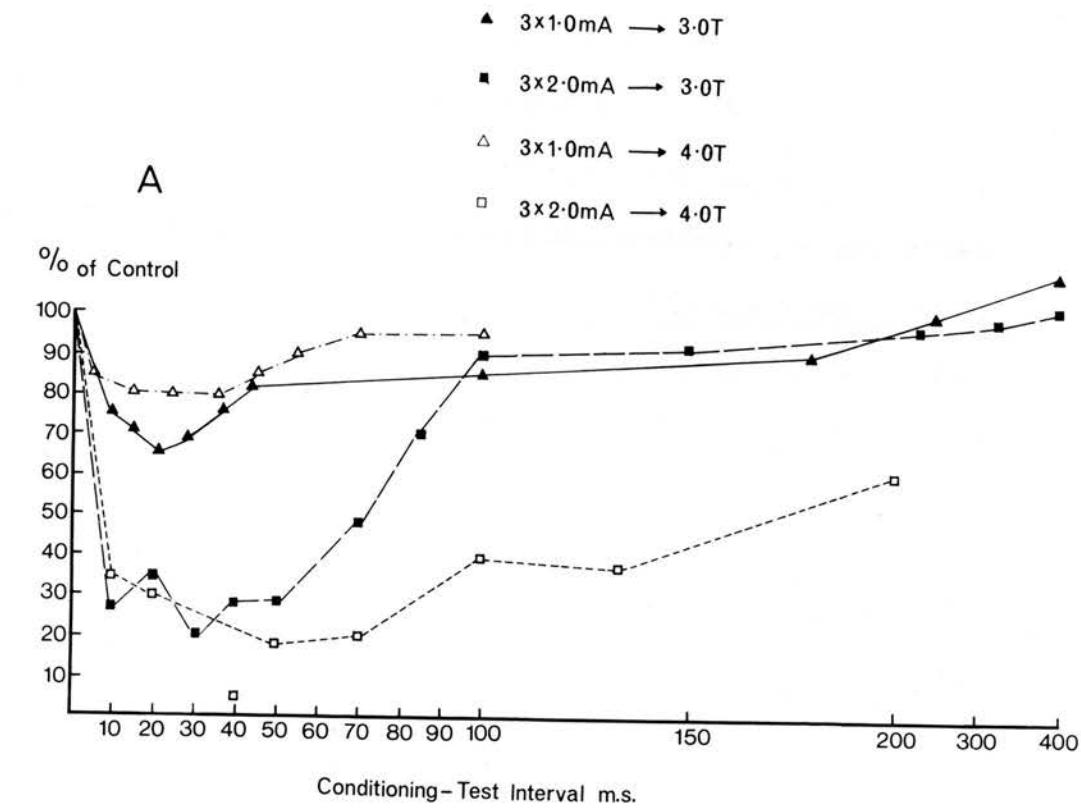
Figure 30

A The time course of inhibition from the forelimb SI area of the contralateral cerebral cortex. The conditioning-test interval was the time between the beginning of the 3 conditioning pulses applied to the cerebral cortex and the beginning of the test stimulus to the superficial radial nerve. Each point plotted represents the ratio of the number of impulses in 5 conditioned and 5 unconditioned impulse trains. Triangles represent 1.0 mA and squares 2.0 mA conditioning pulses.

Black triangles and squares = unit 754301 excited by a 3.0 x T, 0.2 ms pulse.

Open triangles and squares = unit 753901 excited by a 4.0 x T, 0.2 ms pulse.

B The time course of inhibition from the SI forelimb area of the contralateral cerebral cortex (squares) and the SRN (triangles) for unit 754206, a Hair only (Tylotrich) type unit. Time courses were plotted as in A. The test stimulus was a pulse of 3.0 x Threshold. The conditioning pulses were trains of 3, 500 Hz, 0.2 ms., 2.0 mA cortical or 7.0 xT XSRN pulses.


A
3x1·0mA → 3·0T
3x2·0mA → 3·0T
3x1·0mA → 4·0T
3x2·0mA → 4·0T
% of Control
100
90
80
70
60
50
40
30
20
10
10 20 30 40 50 60 70 80 90 100 150 200 300 400
Conditioning – Test Interval m.s.

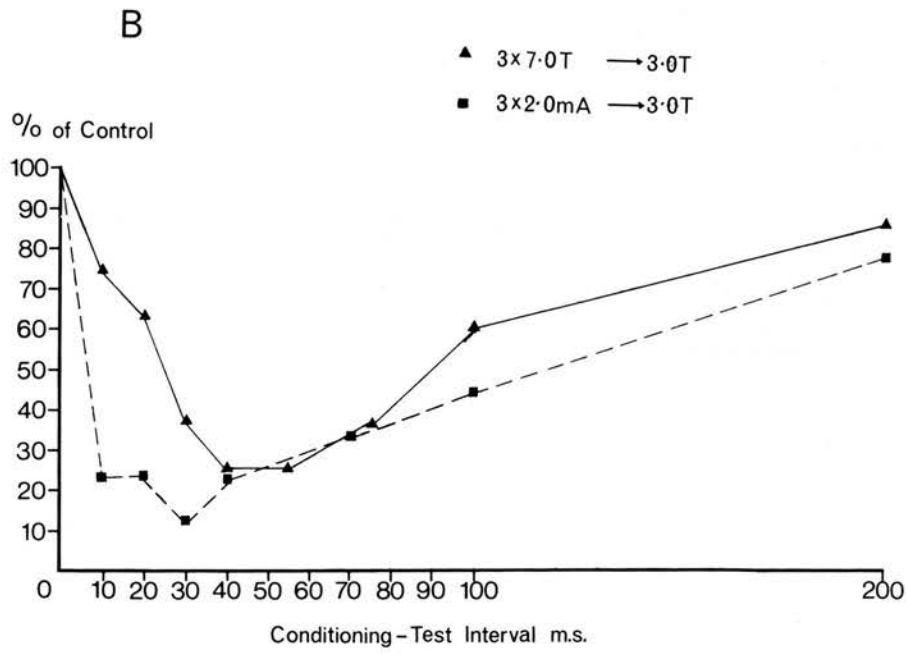

B
3x7·0T → 3·0T
3x2·0mA → 3·0T
% of Control
100
90
80
70
60
50
40
30
20
10
0 10 20 30 40 50 60 70 80 90 100 200
Conditioning – Test Interval m.s.

Figure 31

Time courses of inhibition from ipsilateral and contralateral areas of the cortex. Points were plotted as in figure 30.

A Unit 7620 07 a 'hair only' type unit. The test stimulus was a 4.0 x T, 0.2 ms pulse

Squares = ipsilateral forelimb SI area stimulated with 3, 0.2ms, 500 Hz, 1.0 mA pulses.

Triangles = ipsilateral forelimb SII area stimulated with 3, 0.2ms, 500 Hz, 500 Hz, 1.0 mA pulses.

B Unit 762001 a 'hair and pressure' unit. The test stimulus was a 6.0 x T 0.2ms pulse

3, 0.2ms, 500 Hz. conditioning pulses of 2.0 mA were applied to:

Open Triangles = ipsilateral hind limb SI

Closed Triangles = contralateral hind limb SI

Open Squares = ipsilateral forelimb SI

Closed Squares = contralateral forelimb SI

C Unit 762003 excited by a 5.0 x T 0.2 ms pulse

D Unit 762007 excited by a 4.0 x T 0.2 ms pulse

Both were hair only type units

Triangles = conditioning pulses applied to contralateral forelimb SI

Squares = conditioning pulses applied to contralateral forelimb SII

In C 2.0mA and in D 1.0 mA conditioning pulses were used, both were trains of 3, 0.2ms 500 Hz pulses.

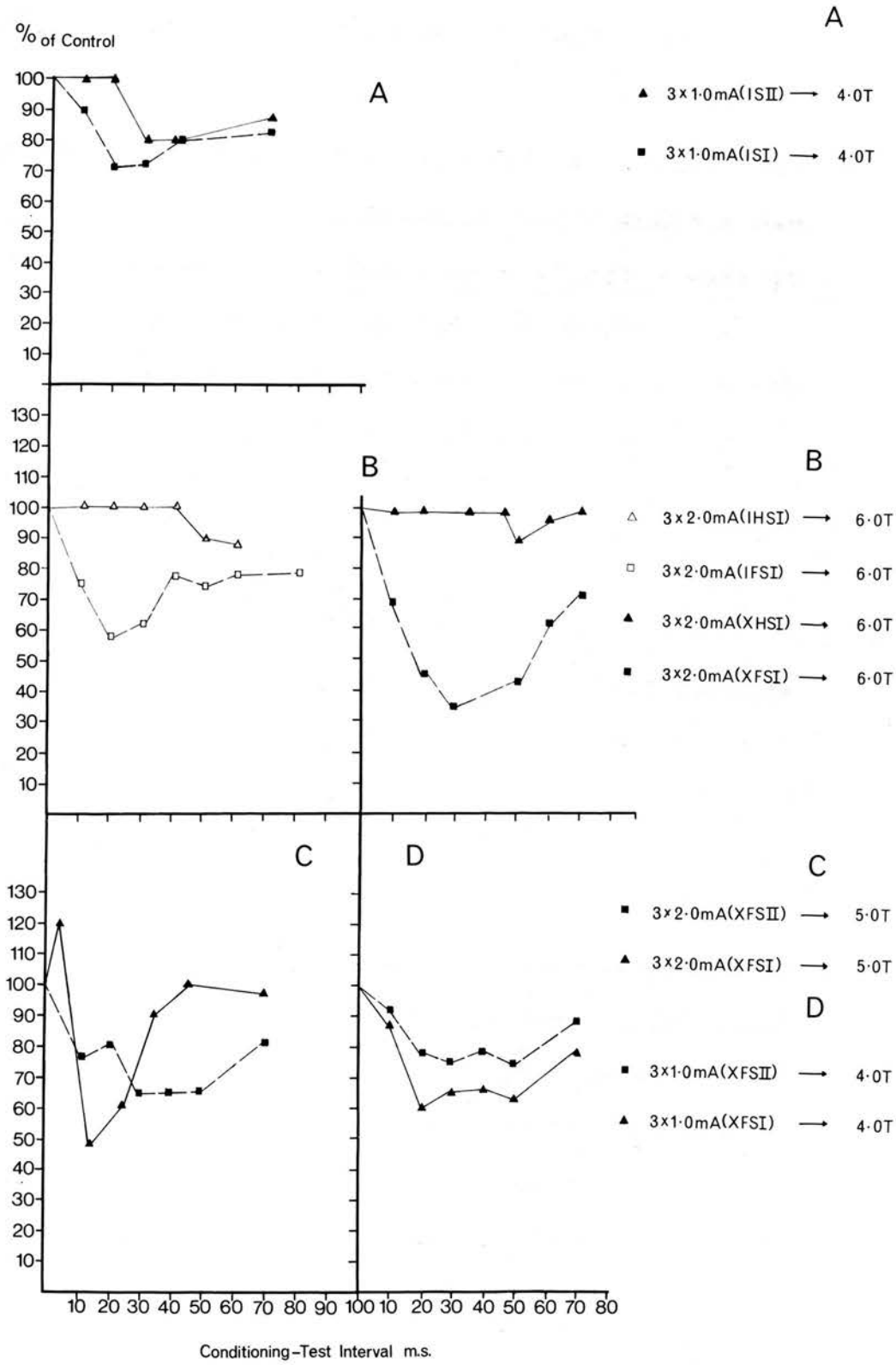

% of Control
A
B
C
D
▲ 3×1·0mA(ISII) ⟶ 4·0T
■ 3×1·0mA(ISI) ⟶ 4·0T
△ 3×2·0mA(IHSI) ⟶ 6·0T
□ 3×2·0mA(IFSI) ⟶ 6·0T
▲ 3×2·0mA(XHSI) ⟶ 6·0T
■ 3×2·0mA(XFSI) ⟶ 6·0T
■ 3×2·0mA(XFSII) ⟶ 5·0T
▲ 3×2·0mA(XFSI) ⟶ 5·0T
■ 3×1·0mA(XFSII) ⟶ 4·0T
▲ 3×1·0mA(XFSI) ⟶ 4·0T
Conditioning–Test Interval m.s.

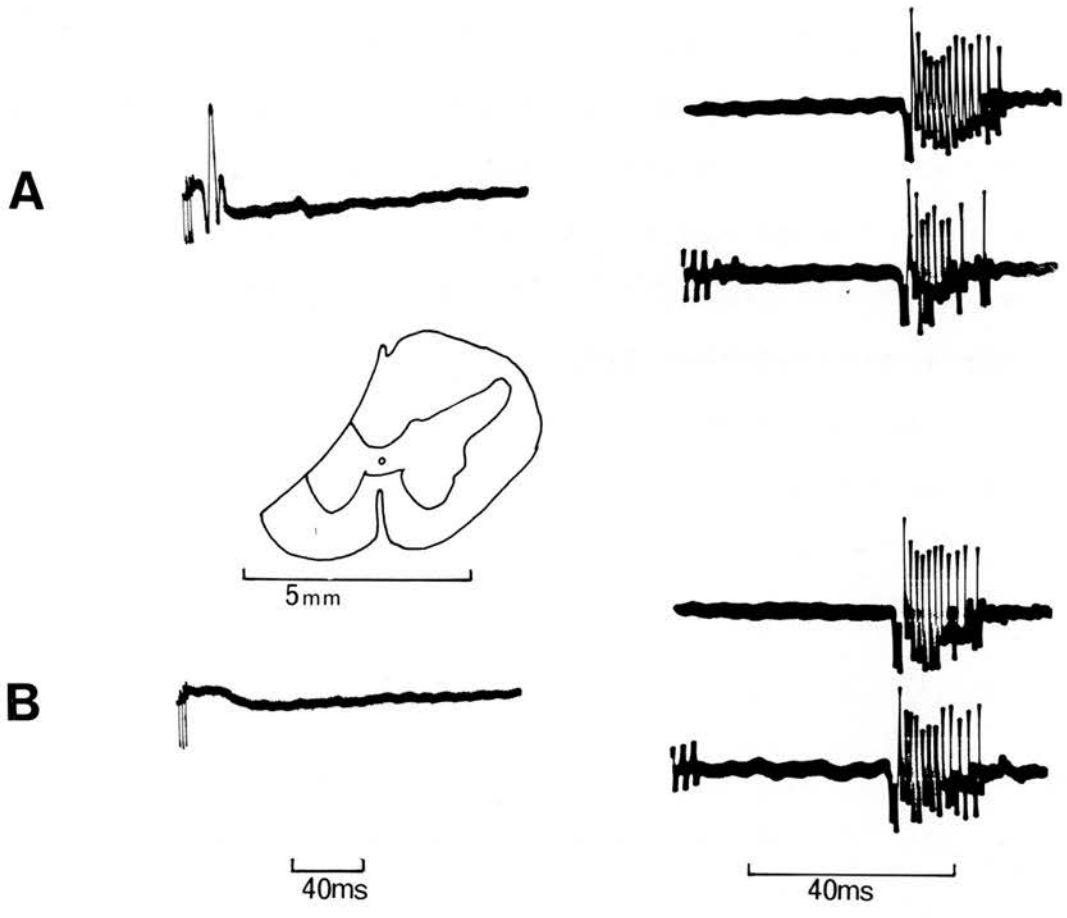
Figure 32

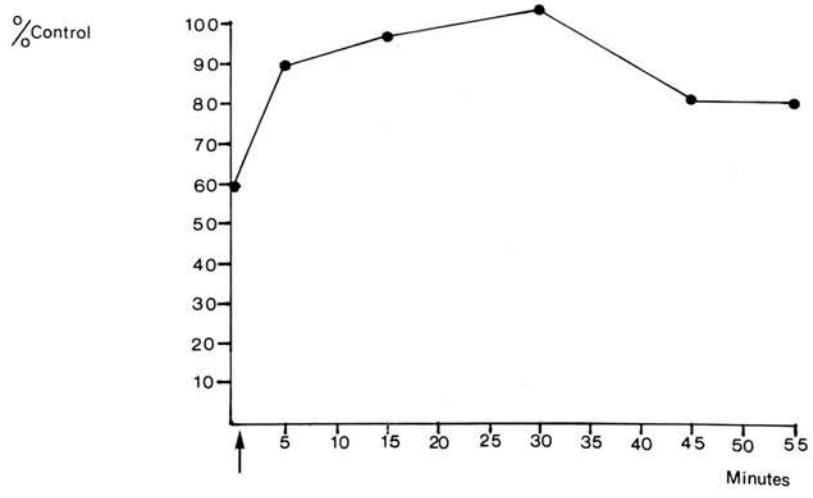
A and B The effect of ipsilateral hemisection upon corticofugal inhibition of transmission through the SCT.

On the left are cord dorsum potential recordings, A before and B after hemisection. The hemisected cord was sectioned after the experiment. A fixed, unstained section was traced under a photographic enlarger to show the extent of the lesion.

On the right are the control and conditioned response of an SCT cell to 3, 0.2ms 2.0 mA pulses, before A and after B hemisection. The conditioning stimuli were applied to the contralateral forelimb SI area at a conditioning-testing interval of 40ms.

C shows the time course of inhibition of a SCT unit to 3, 500 Hz., 0.2ms, 2.0mA conditioning pulses applied to the contralateral forelimb SI area before and after the intravenous injection of 10mg Sodium thiopentone (arrow). Each point represents the ratio of 5 conditioned and 5 unconditioned responses. The conditioning-testing interval was 35ms.


A
5mm
B
40ms
40ms


%Control
100
90
80
70
60
50
40
30
20
10
5
10
15
20
25
30
35
40
45
50
55
Minutes

C

Figure 33

Microstimulation of the cortex used to inhibit an SCT cell discharge. 6, 0.2ms 500 Hz pulses were applied to the same spot, 1,000 µm beneath the surface of forelimb receiving area SI, to condition discharges evoked by stimulation of the superficial radial nerve.

A 5 control responses to electrical stimulation of the superficial radial nerve.

B The responses conditioned by 100µA anodal pulses

% inhibition = 14%

$P < 0.05$

C The responses conditioned by 100 µA cathodal pulses

% inhibition = 40%

$P < 0.001$

D The responses conditioned by 50 µA cathodal pulses

% inhibition = 51%

$P < 0.001$

E The responses conditioned by 25 µA cathodal pulses

% inhibition = 14%

$P < 0.02$

The current monitor trace is photographically blurred. The conditioning testing interval is 33ms in all traces.

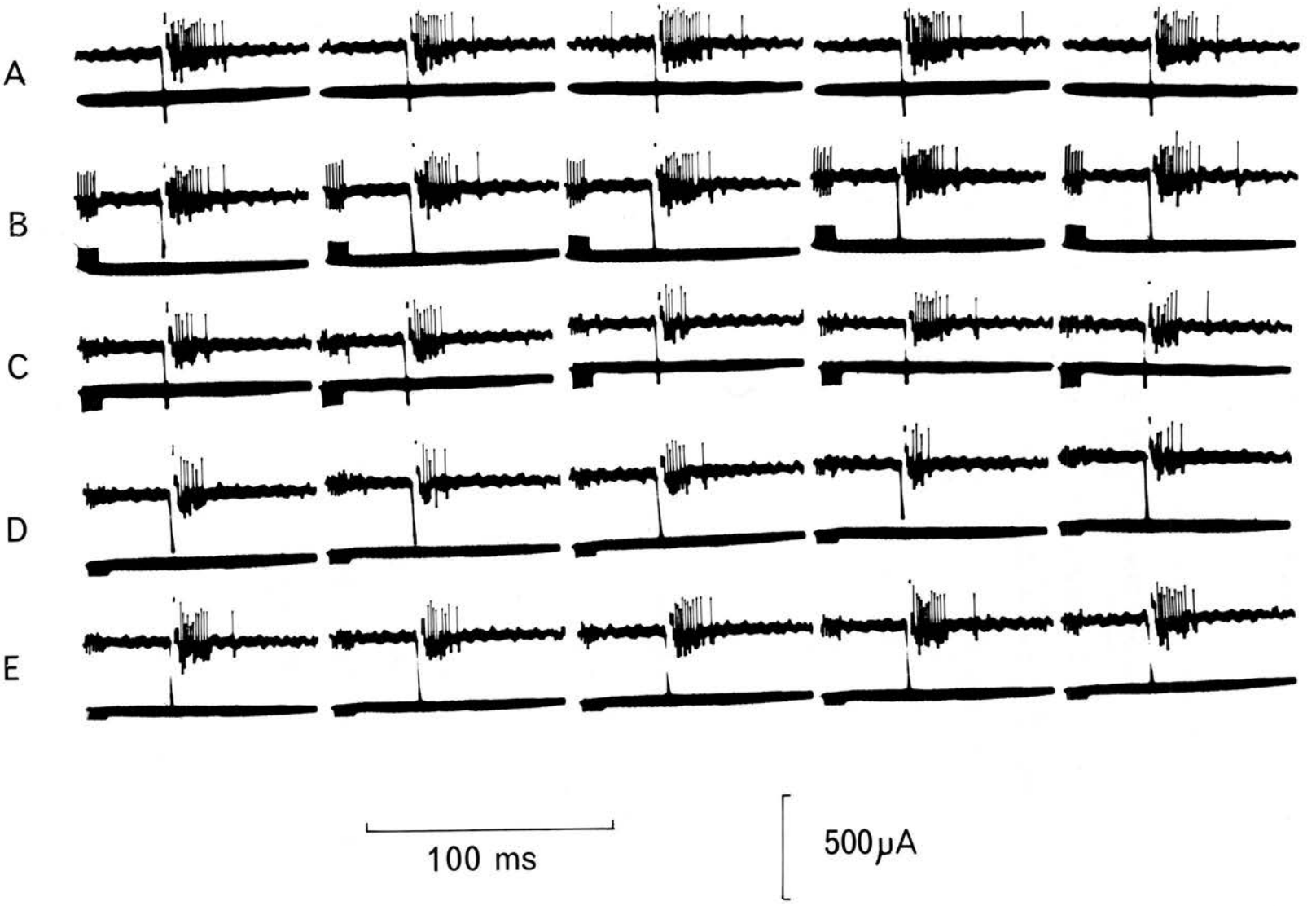

A
B
C
D
E
100 ms
500μA

Table 8

This summarises some of the data of Section IV. The 30 units are arranged chronologically downwards. The first 4 digits of the unit number is the experiment's number.

Receptive fields were identified as:

H — Responding to brushing of hairs only. (T) and (G) denote that the unit was further identified as being excited by Tylotrich or Guard hairs.

H & P — Responding to brushing of hairs and the application of a sprung metal clip.

P — Responding to pinch or pressure only.

The presence of inhibition is denoted by +.
The absence of inhibition is denoted by -.

The sources of inhibition are denoted as X or I being contralateral or ipsilateral to the recording electrode respectively. Inhibition was never elicited from either medial plantar nerve.

Unit	R.F. type	Inhibition from XSI	XSII	ISI	ISII	XSRN	MPN	
753901	H	+	+			+	−	
02	None	+				+	−	
754001	H	+	+			−	−	
02	H	+	+			+	−	
04	H&P	+	+			+	−	
05	P	+	+			+	−	
754101	H(T)	+	+			+	−	
04	H&P	+	+			+	−	
05	H(T)	+	+			+	−	
754201	H(T)	+	+			−	−	
04	H&P	+	+			+	−	
06	H(T)	+	+			+	−	
754301	H	+	+			+	−	
754401	H(T)	+	+	−	−	−	−	
761301	H(T)	−	−	−	−	−	−	
02	H	+	+			+	−	
03	H	+				+	−	
04	H&P	−	−			−	−	
761701	H	+	+	+	+	+	−	
02	H	+	+			+	−	
03	H&P	−	−	−	−	−	−	
04	H&P	−	−			−	−	
05	H	+	+	−	−	−	−	
06	H	+	+	+	+	+	−	
762001	H&P	+	+	+	+	+	−	
02	H&P	−	−			+	−	
03	H	+	+	+	+	+	−	
04	H	+	+	+	+	−	−	
06	H	−	−	−	−	−	−	
07	H(G)	+	+	+	+	+	−	

inhibition at depths of 1000 and 1500μM respectively (Figure 33).

Cathodal pulses were much more effective than anodal in eliciting inhibition when micropipettes were used as conditioning electrodes.

Discussion

The results of this section show that most spino-cervical tract units with receptive fields in the distal forelimb may be subjected to inhibition by electrical stimulation of certain parts of the cerebral cortex. (Table 8)

Two points of interest arise out of the finding that six units could not be inhibited from the cortex. Firstly there is the question of whether these units were really not subjected to corticofugal influences or if this was simply due to poor experimental conditions. Second is the finding that 50% of the 'hair and pressure' units encountered could not be inhibited from the cortex compared to only 10% of the 'hair only' sample.

In preliminary experiments not reported in this thesis, cats in which there was no corticofugal inhibition on the spino-cervical tract were encountered when the physiological state of the animal was, in terms of the observed blood pressure, visually observed circulation, body temperature and expired CO2, otherwise satisfactory. Hence it may be that corticofugal inhibition is a more sensitive pointer to the physiological state of the central nervous system than any of the normally observed parameters. A similar

observation was made by Brown and Martin (1973) concerning the presence of segmental inhibition on the spino-cervical tract. However the finding that all but one of the cortically non-inhibited units came from experiments in which cortically inhibited units were subsequently found, coupled with the observation that one of the cortically non-inhibited units was subject to segmental inhibition favours the possibility that some spino-cervical tract cells are not influenced from the cerebral cortex.

In the monkey Coulter Maunz and Willis (1974) have shown that intracortical stimulation of the hind limb area of the pericentral cortex leads to inhibition of the input from low threshold mechanoreceptive spinothalamic tract cells in preference to those with inputs from noxious or thermal stimuli.

If indeed this is the case then the preferential inhibition of 'hair only' units may be of some functional significance. Horrobin (1966) found that relay cells in the lateral cervical nucleus had many more receptive fields of the 'hair only' type than would be expected from a comparison with the input to this nucleus as revealed in Section II of this thesis. Thus it may be that the cerebral cortex is more concerned with monitoring information from units with hair only receptive fields than from other types of unit.

The lack of inhibition from hind limb and forelimb nerves relative to those reported in section III can be attributed to the anaesthetic as this is known to depress

inhibition (Brown and Franz, 1969). It was suggested in Section III that inhibition from hind limb sources operates via a brain stem loop. As this inhibition was always absent it may be that this loop contains synapses labile to the anaesthetic chloralose.

Similarly the finding of reversible release of corticofugal inhibition after intravenous injection of the short acting barbiturate sodium thiopentane, confirms the observation of Brown and Short (1974) that sodium pentobarbitone, another barbiturate, removes corticofugal inhibition on the spino-cervical tract and adds weight to the argument that previous attempts to demonstrate corticofugal inhibition were due to the choice of barbiturate anaesthesia (Lundberg, Norrsell and Voorhoeve, 1963).

The topographical results of this section are complementary to those of Brown and Short (1974). These authors found that the areas of contralateral cortex eliciting maximal inhibition on spino-cervical tract axons with hind limb receptive fields corresponded with the hind limb receiving areas. The present section supports the hypothesis that the corollary, namely that spino-cervical tract units with receptive fields on the forelimb are preferentially inhibited from the forelimb receiving area, also holds.

Both studies found inhibition from the contralateral face area. There are two possible explanations for this phenomenon.

(1) it is due to spread of stimulating current from the forelimb and hind limb areas.
(2) there is a true source of cortico-fugal inhibition within the face area.

The present findings cannot conclusively distinguish between these alternatives. The finding that 1.0 μA pulses are rarely effective from the face area would favour the first alternative although the results of surface stimulation are not sufficient evidence.

The second alternative is intuitively attractive as Peto (1974) has demonstrated cortico-fugal inhibition on lateral cervical nuclear cells from the face area. However the finding of inhibition following stimulation of the forelimb S.II area mitigates against the possibility that the effects which Brown and Short (1974) obtained from the hind limb S.II area were due to spread of current to the face area.

Two notable discrepancies between the studies are:
(1) the apparent lack of facilitation of forelimb units. Brown and Short (1974) found facilitation from the caudal surface of the Ansate sulcus which in the present study yielded inhibition with 2.0 mA pulses.
(2) The methodological difference that Brown and Short (1974) used a constant voltage stimulus, the voltage being that which elicits 50% inhibition from the S.I receiving area. This could explain the more pronounced effects from S.II found in this study particularly if the degree of inhibition of different units is a non-linear function of the voltage

stimulus. This is more likely to occur for inhibitory areas buried in the lip of the cruciate sulcus than for those lying in uninvaginated parts of the cortex.

The finding of inhibition from the ipsilateral cortex has not previously been reported in the literature on the spino-cervical tract. As the second ipsilateral receiving area is known to have a bilateral input inhibition from this region was not as unexpected as that from the ipsilateral first receiving area. When considering ipsilaterally evoked inhibition 4 possibilities should be borne in mind:

(1) there is a true inhibitory centre in the ipsilateral cortex.

(2) the inhibition is mediated from the contralateral cortex via transcallosal fibres.

(3) the effect is due to spread of stimulus current to the contralateral hemisphere.

(4) Both effects occur because of stimulus spread to separate or common subcortical structures.

The third possibility is unlikely because the hind limb areas of the ipsilateral cortex, which are closer to the contralateral hemisphere did not mediate inhibition. The fourth possibility, in the light of the depth stimulation results, is also unlikely.

Thus the first two explanations appear most reasonable. It is known on both anatomical and physiological grounds that transcallosal fibres tend to tie up the mid-line of the body and that most of them have wide, bilateral receptive fields. Why then they should convey inhibition

on spino-cervical tract units with extremely distal receptive field locations is not clear and makes the first possibility intuitively more attractive. However a definitive answer to this question would require section of the corpus callosum.

The time course of inhibition from contralateral S.II differs with that from contralateral S.I in a manner suggestive of the hypothesis that inhibition elicited from S.II is mediated via S.I. Brown and Short (1974) attempted to cool S.I. but were unable to release the inhibition from S.II. Because of the greater proximity of the forelimb first and second receiving areas this technique was not attempted.

The weak, delayed inhibition seen from the contralateral hind limb areas could be accounted for by polysynaptic excitation of inhibitory centres as the length of the delay would seem too long to be caused simply by spread of stimulating current.

It is difficult to correlate the results of surface stimulation with cytoarchitectonics, as the locations of the cells upon which the stimulus is acting are unknown. However areas 3a and 4γ of Hassler and Muhs-Clement (1964) appear to be good candidates and the results of stimulating in depth in these areas are consistent with their implication.

The finding that inhibition was elicitable from the contralateral forelimb cortex at current strengths of 25 μA and at depths of 1500 - 2000μm suggests that surface

stimulation is activating, at least in part, cells in the grey matter. However the degree of inhibition seen with such stimulating techniques was never as great as that seen from the surface. Thus it is possible that surface stimulation is either activating more than one inhibitory locus or that fibres in the white matter of the cortex are also being excited. The observation that cathodal currents are more effective for microstimulation is compatible with the results of Asanuma and Sakata (1967) whilst the observation that they are also more effective from the surface is in keeping with Phillips (1956) observation that superficial cells are more readily excited by surface negative pulses.

All the S.C.T. units recorded from in this section were activated from the superficial radial nerve. They thus tended to have receptive fields on the distal medial forepaw and may represent an uneven sample of the forelimb S.C.T. component. The ratio of hair only to other unit types was even greater than in the sample reported in section II.

The depths at which units were encountered are consistent with their location in Laminae IV and V. No difference was found in the depths of hair only and hair and pressure units as might be expected from Wall's (1967) theory of the laminar organisation of the lumbo-sacral spinal cord. Neither was any difference in corticofugal inhibition noticed between units with different receptive field sizes or types.

Unlike hind limb spino-cervical tract units, which are

located in or adjacent to the spinal segments containing the dorsal rootlets of their excitatory afferents (Bryan, Coulter, Trevino and Willis, 1973), forelimb spino-cervical tract units appear to be located rostral to the entry zones of their excitatory afferents. According to anatomical (Reighard and Jennings, 1961) and physiological (Hekmatpanah, 1961) evidence the superficial radial nerve enters the spinal cord through the dorsal rootlets C7 to T1. Thus estimates of the mono or polysynaptic nature of the excitatory connections to spino-cervical tract cells, based solely on latency measurements are unreliable due to the long conduction distances. It may be that the spatial separation of interacting neural elements is a peculiar feature of the organisation of the cervical enlargement. Oscarsson (1964) states that the relay of primary afferents with the cells of origin of the rostral spino-cerebellar tract occurs "at, or slightly above, the level of the dorsal root entrance" and Illert and Lundberg (1975) have shown a more rostral location of Ia inhibitory internurones acting on motorneurones in the cervical enlargement.

The long time course of cortically induced inhibition and segmental inhibition suggest that both sources act presynaptically. The presence of action potentials evoked in spino-cervical tract cells by cortical stimulation and the greater degree of inhibition seen from the cortex suggests that the corticofugal fibres have either a separate inhibitory circuit or have better access to the same inhibitory circuit (i.e. acting on more proximal synapses).

Carpenter, Lundberg and Norrsell (1962) and Brown and Short (1974) who also observed these cortically evoked action potentials attributed them to an intense primary afferent depolarisation analogous to the dorsal root reflex. If this is so then the corticofugal pathways are likely to inhibit presynaptically primary afferent fibres which have monosynaptic connections with spinocervical tract cells. This is probable for two reasons:

(1) the safety factor of transmission might not suffice for more than one synapse.

(2) the relatively short latencies of the earliest cortically evoked action potentials are compatible with monosynaptic connections. Assuming a conduction distance of 15 cm and a conduction velocity of 50 ms^{-1} this leaves for the observed case of a 7.0 ms latency, 4.0 ms for synaptic transmission.

Furthermore if the two spino-cervical tract units receiving total corticofugal inhibition were monosynaptically excited from the superficial radial nerve and presynaptically inhibited from the cortex then the inhibitory synapse must be on a monosynaptic connection.

However the finding that corticofugal inhibition, like segmental inhibition, is most effective on the last few action potentials in each impulse train suggests that the polysynaptic connections are most susceptible to cortico-fugal influences. Brown, Kirk and Martin (1973) have invoked such a mechanism to explain segmental inhibition. They did not report total inhibition of discharges or

action potentials evoked by stimulating 'non-excitatory' nerves. The time to peak of cortico-fugal inhibition on relay units in the cuneate nucleus (Cole and Gordon, 1976) is 10-20 ms shorter than that on cervical spino-cervical tract cells. This difference must reflect a functional asymmetry between the two ascending systems as the difference in conduction distance will only account for a discrepancy of 1 or 2 ms in the time course.

If the cessation of inhibition following partial ipsilateral hemisection is a result of interruption of descending pathways then the rubro or cortico-spinal tracts or both may be the mediators. Fetz (1968) found inhibition of lamina IV cells following stimulation of the pyramidal tracts and Hongo and Jankowska (1967) found that stimulating the hind limb sensory cortex elicited primary afferent depolarisation in the lumbosacral cord of pyramidotomised cats. Atkinson, Seguin and Weisendanger (1975) have suggested that cortico-spinal fibres whose cell bodies are in the contralateral S.II may be influencing ascending fibres.

In the cervical spinal cord both the rubro-spinal and cortico-spinal tracts excite common interneurones (Bayer and Kostyuk, 1973). Whether these interneurones are responsible for the cortico-fugal inhibition seen in this study is not known. Intracellular studies are needed to resolve the inhibitory mechanisms and pathways acting on cervical spino-cervical tract cells.

Section V

Conclusion and General Discussion of the Function of the Spinocervical Tract

GENERAL DISCUSSION

Qualitatively the forelimb component of the spino-cervical tract is similar to its hind limb counterpart. However quantitatively it differs in two respects: namely that it contributes a greater proportion of the input to the lateral cervical nucleus than either the trunk or hind limb components and it contains a significantly greater proportion of units with hair only receptive fields.

No evidence was found for a projection of either the carpal tactile hairs or the slowly adapting type I units.

In a sample of axons in the medial lemniscus, Brown, Gordon and Kay (1974) found that 88% of the units had forelimb receptive fields. Two of these units had receptive fields typical of the slowly adapting type I receptors. As these authors felt that the majority of their sample was in the dorsal column nuclear projection and as Uddenberg (1968a) has described slowly adapting type I units in the Fasciculus Cuneatus it is probable that the dorsal columns and possible that the cuneocerebellar tract convey information from these receptors.

Inhibitory receptive fields for forelimb spino-cervical tract units are analogous to those described by Brown (1968b) for the hind limb component. In decerebrate cats strong pinch or pressure at the base of the tail or ipsilateral hind limb will inhibit some units with fore-limb receptive fields as will electrical stimulation of the medial plantar nerves. In spinal cats electrical stimulation of the contralateral superficial radial nerve

is a more potent mediator of segmental inhibition but no inhibition is elicitable from hind limb nerves. Thus it is likely that inhibition of forelimb units from the hind limb is mediated through a loop involving structures rostral to the spinal cord. In intact animals this limb-limb inhibition is not present. This could be due either to the anaesthetic chloralose or to tonic disinhibition from parts of the brain rostral to the colliculi.

Stimulating the forelimb receiving areas of both cerebral hemispheres and in particular the contralateral hemisphere is a particularly effective means of inhibiting spinocervical tract cells in the cervical spinal cord.

Such inhibition exhibits a longer time to peak than corticofugal inhibition of cells in the cuneate nucleus (Cole and Gordon, 1976) and has a duration more compatible with a pre-synaptic than a post-synaptic mechanism. The observation of action potentials evoked in spino-cervical tract cells by conditioning stimuli applied to the cortex but not the peripheral nerves is also explicable as a manifestation of presynaptic inhibition and may indicate that the cortex has access to more direct inhibitory pathways than the segmental nerves.

The areas of contralateral cortex most effective in inhibiting transmission through the forelimb and hind limb components of the spino-cervical tract are topographically distinct and overlap with:

(1) those areas for which discrete forelimb and hind limb movements may be elicited in awake cats (Nieoullon and

Rispal-Padel, 1976),

(2) the classical forelimb and hind limb receiving areas.

It is possible that corticofugal activity in the spino-cervical system operates through a closed loop, by which long ascending tracts activate the descending inhibitory fibres. However the operational latency of such a loop would be of the order of 50 ms and thus may be too long for use in movement. It is more probable that corticofugal activity is initiated from higher centres. Ghez and Lenzi (1970) and Coulter (1974) have shown a decrease in medial lemniscal activity prior to movement.

There are a number of speculations in the literature regarding the function of the spino-cervical tract and of the inhibitory systems acting on it.

Taub (1964) suggested that:

(1) the feline spino-cervical tract may be equivalent to the spinothalamic tract of primates, and

(2) that it alerts the animal to pain stimuli thus initiating descending inhibition on the afferent input.

There are now a number of experimental results pertinent to this hypothesis. Andersson, Norrsell and Norrsell (1972) found that in the cynomologous monkey a pathway in the contralateral ventral spinal cord must be sectioned to eliminate short latency, surface positive cortical evoked potentials, whilst Andersson (1962) had previously found that in the cat the equivalent pathway lay in the ipsilateral dorsolateral funiculus. Anatomical evidence (Boivie, 1971) also shows the spino-thalamic

tract to be relatively poorly developed in the cat. Some of the results of behavioural experiments on cats may also be interpreted favourably in the light of this hypothesis. In particular Kennard's (1954) observation that section of the dorsolateral funiculus abolishes responses to a presumably nociceptive stimulus. The electrophysiological results of Hamann (1974) showed that spino-cervical tract units do indeed convey information from cutaneous afferents with conduction velocities in the A and C range and that the discharges evoked by these fibres are most effectively inhibited by descending systems.

As Andersson (1962) showed that the tract with the fastest access to the cortex from the hind limb lies in the ipsilateral dorsolateral funiculus Taub's second hypothesis is also attractive.

However some findings are difficult to reconcile with Taub's theory. From the forelimb receptive fields the dorsal columns convey short latency surface positive potentials to the cortex as fast if not faster than the spino-cervical system (Oscarsson and Rosén, 1966), and yet the forelimb component of the spino-cervical tract is quantitatively more important than the hind limb component. In decerebrate and possibly in anaesthetised cats tonic descending inhibition diminishes the responsiveness of spino-cervical tract cells to nociceptive stimuli (Brown, 1968b) and most authors have found that the majority of units have small receptive fields which are adequately excited by very light tactile stimuli. It is difficult

to see how these receptive fields could help to alert the animal to painful stimuli or how the asymmetric and disparate inhibitory receptive fields would be of use in this.

Hongo, Jankowska and Lundberg (1968) have proposed that the spino-cervical system might function as a detector of movement across the surface of the skin. Their evidence for this was the presence of inhibitory post synaptic potentials elicited from small receptive fields adjacent to the excitatory field. Again, however, the presence of many inhibitory receptive fields widely separated from the excitatory field is difficult to reconcile with this hypothesis. Intuitively the surround type of inhibition seen in some cells in the dorsal column nuclei (Gordon and Jukes, 1964) but never reported in the spino-cervical system would seem better suited to fulfil this function. Indeed Vierk (1973, 1974) working on monkeys found that section of the dorsal columns was associated with lack of direction detection of light tactile stimuli. He suggested that the dorsal column system acted as an edge detector whilst other ascending sensory tracts including one in the dorsolateral funiculus acted by counting receptive fields in different locations.

Other behaviour experiments performed on different animals and by different workers have suggested different functions for the spino-cervical system. Kitai and Weinberg (1968) have suggested that roughness discrimination is impaired in cats with lesions in the dorsolateral

funiculus. Norrsell (1966) found that conditioned reflexes to cutaneous stimuli were impaired after the dog's spino-cervical tract was cut.

The observation that descending inhibition most profoundly inhibited the poly rather than the monosynaptic input to spino-cervical tract cells led Brown, Kirk and Martin (1972) to propose that one function of descending inhibition could be "to focus the attention of the central nervous system on the monosynaptically produced discharges, in particular to compare the times of arrival of these discharges at some central destination." Presumably segmental inhibition could also help to modulate the polysynaptic input in situations where the inhibitory receptive fields were adequately stimulated. The results of section II of this thesis would suggest that the lateral cervical nucleus is receiving simultaneously information of events occurring at different locations and times.

If this hypothesis is extended further it is pertinent to ask two questions:

(1) what kind of information is thus eliminated from the spinocervical system? and

(2) in what situation would the remaining information be of use?

Hamann (1974) provided a partial answer to the first question by studying the effects of descending systems on units with or without an A or C fibre input. He found that the excitation from these two fibre types was most

effectively inhibited by segmental sources thus leaving the spino-cervical pathway clear for information from large myelinated fibres, notably the type T and G hair follicle receptors of Brown and Iggo (1967). Brown (1971) studied the effects of descending inhibition in decerebrate cats made reversibly spinal by cooling the spinal cord. He found that in the decerebrate state the higher threshold inputs to spino-cervical tract units were inhibited. Thus a cell which responded to hair movement and pressure in the spinal state might only respond to hair movement in the decerebrate state. Paradoxically it seems from the results of section IV of this thesis that corticofugal inhibition is directed preferentially towards the hair only units and is less effective aginst hair and pressure units. This could be because the cortex is involved in monitoring information which is useful to itself e.g. hair movement and leaves the more caudal parts of the nervous system to monitor information from receptors responding to pinch, pressure, joint and muscle movement. This latter information may be simply a redundant product of the evolution of the spinocervical system or it may have a function to play at a segmental level. Snow, Rose and Brown (1976) have shown that spino-cervical tract axons give off collaterals to the dorsal horn; thus it is possible that they have segmental actions.

An answer to the second question requires further speculation; one attractive possibility is that the hair receptors are involved in regulating movement, in

particular running movement. There are a number of observations which lend support to this notion. Oscarsson and Rosen (1966, 1968) pointed out that the spino-cervical tract projects to a more rostral part of the cat's sensory-motor cortex than the dorsal column system and thus may have a greater degree of overlap with the motor cortex. Rapidly adapting receptors such as those from the tylotrich and guard hair follicles may well act as velocity detectors and thus help to co-ordinate movements. Norrsell (1966) showed the spino-cervical system was involved in conditioned reflexes from air puffs to hairy skin.

As judged by the size of the lateral cervical nucleus the spino-cervical system is most prominent in carnivores which exhibit goal directed running whilst it is relatively redundant in rodents and primates which normally run only to escape their predators. Thus for carnivores a fast pathway to the motor cortex for rapidly adapting movement detectors would appear more important than the presence of a surround inhibition system or of slowly adapting receptor inputs.

Recently, in adult cats, cutaneous receptors in the superficial radial nerve have been shown to affect postural reflexes (Regis, Trouche and Massion, 1975). Thus cutaneous systems could play a role in motor control at the segmental level as well as via the motor cortex. Implicating the spino-cervical tract in motor control would help to explain the nature of its inhibitory receptive

fields and segmental inhibition which bear greater similarities to those of motorneurones than to other sensory neurones.

Peto (1974) found that the facial area of the cat's first contralateral sensory cortex inhibited the deafferented lateral cervical nuclear cells he recorded from. Other areas of the cortex were less effective. He also made the comparative observation that there was an inverse relationship between the sizes of the lateral cervical nuclei and the trigeminal nuclei in different species. Thus animals which rely on a stationary food source e.g. rodents and primates, would require less tactile information to regulate their movement than animals which stalk their food, e.g. cats. Conversely when a carnivore is feeding or when its head is stimulated it can switch attention away from its body by inhibiting the lateral cervical nucleus.

Unfortunately this hypothesis is very difficult to test experimentally. One possible approach would be to record spino-cervical unit discharges with chronically implanted electrodes and study their variation with different types of movements.

Thus it is proposed that the spino-cervical system may act at two levels:

(1) at a cortical level to monitor the activity of velocity detecting rapidly adapting receptors such as hair follicle afferents and possibly use this information for motor control,

(2) at a segmental level, dealing with higher threshold inputs such as pinch, pressure and joint movements. This function may be more directly linked with posture and motor control in the spinal cord.

SECTION VI

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